Body reconstruction and size estimation of plesiosaurs

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Abstract

Body size is the key to understanding many biological properties. Sizes of extinct animals are usually estimated from body reconstructions since their masses can not be weighed directly. Plesiosaurs were Mesozoic marine reptiles that were diverse in both body plan and size. Attempts to estimate body masses of plesiosaurs were rare in the past two centuries, possibly due to lack of knowledge about their postcranial anatomy and body shapes in life. The burst of plesiosaur studies in the past two decades has greatly expanded our cognition of their physiology, taxonomy, potential behavior and even soft body outlines. Here I present a comprehensive review of relevant knowledge, and propose a uniform set of methodology for rigorous body reconstruction of plesiosaurs. Twenty-two plesiosaur models were constructed under these criteria, and they were subsequently used as samples to find proxies for body mass. It is revealed that multiple skeletal elements are good indicators of plesiosaur size. This study offers scaling equations for size estimation, enabling quick acquisition of body mass information from fragmented fossils. A summary of body size evolution of different plesiosaur clades is also provided.

Contents

1 Introduction **3**
1.1 Institutional abbreviations . . . 4
1.2 Unit abbreviations . . . 4

2 Preliminaries to plesiosaur reconstruction **4**
2.1 Postcranial anatomy of plesiosaurs . . . 5
2.1.1 Vertebral column . . . 5
2.1.2 Rib cage . . . 10
2.1.3 Limbs . . . 12
2.2 Soft tissue reconstruction . . . 13
2.2.1 Plesiosaur fossils with soft tissues . . . 13
2.2.2 Head and neck . . . 14
2.2.3 Rib cage . . . 15
2.2.4 Tail . . . 18
2.2.5 Flipper profile . . . 18
2.3 Inconsistent definitions and measuring criteria . . . 18
2.3.1 Skull . . . 18

2.3.2 Spinal segmentation . . . 20
2.3.3 Ribs . . . 20
2.4 Ontogeny . . . 21
2.5 Phylogeny and Taxonomy . . . 21
2.6 A review of plesiosaur body mass estimation . . . 22

3 Reconstructing missing puzzles in plesiosaur fossils 23
3.1 Skull size . . . 24
3.2 Rib length . . . 25
3.3 Tail length . . . 25
3.4 Trunk length . . . 26
3.5 Limb length . . . 26

4 Criteria for plesiosaur reconstruction 26
4.1 Body length calculation . . . 26
4.1.1 Length of vertebral column . . . 27
4.1.2 Skull length . . . 27
4.2 Rib cage reconstruction . . . 28
4.2.1 Glenoid cross-section . . . 28
4.2.2 Acetabulum cross-section . . . 28
4.2.3 Maximum cross-section . . . 28
4.3 Flipper elements . . . 29
4.4 Soft tissue reconstruction . . . 29
4.4.1 Skull and neck . . . 29
4.4.2 Rib cage . . . 29
4.4.3 Tail and flippers . . . 30
4.5 Body density . . . 30

5 Methods 31
5.1 Model construction . . . 31
5.2 Body volume and surface area calculation . . . 31
5.3 Morphometric analysis . . . 32
5.4 Regressions . . . 32

6 Results 33

7 Discussion 34
7.1 On some large Jurassic pliosaurs . . . 34
7.2 A brief summary of plesiosaur body size evolution . . . 38
7.2.1 Rhomaleosauridae . . . 38
7.2.2 Pliosauridae . . . 39
7.2.3 Microcleididae and basal Plesiosauroidea . . . 40
7.2.4 Cryptoclididae . . . 41
7.2.5 Elasmosauridae . . . 42
7.2.6 Polycotylidae . . . 44
7.2.7 Leptocleididae and freshwater plesiosaurs from China . . . 44
7.3 Enlightment for future studies . . . 45

8 Conclusions 46

9 Acknowledgements 46

1 Introduction

Body size is one of the most important biological properties, which is the key to understanding various aspects of an animal, including physiology [1, 2, 3, 4] and ecology [5, 6, 7]. Among all proxies for body size, mass has the advantage over linear measurements that it enables comparison among different taxa without being affected by distinct body proportions. While the masses of extant animals can be weighed directly, those of extinct species are unavailable in most cases. Numerous methods have been developed to estimate the body masses of extinct animals for this reason. One category of methods requires rigorous body reconstructions and transforms them into masses using physical laws, mathematical calculation or computer techniques [8, 9, 10, 11, 12]. Another category, namely scaling methods, advocates digging the relationships between skeletal elements and body mass using regressions [13, 14, 15]. Each category of mass-acquring method has its strengths and shortcomings [16]. Mass estimates based on reconstructions were included as sample data for scaling in some previous studies (e.g., [17, 18]). These methods were termed as "hybrid approaches" in [16].

Plesiosaurs were a group of extinct aquatic reptiles which possessed a cosmopolitan distribution and a wide stratigraphic range [19, 20]. They first appeared in the latest Triassic [21], radiated in Jurassic and Cretaceous [22, 23], and finally went to extinction at the end of Mesozoic together with non-avian dinosaurs [24]. Since the discovery of the first plesiosaur two centuries ago, these animals have been known for their diverse body plans, which were traditionally divided into two morphotypes: long-necked, small-headed "plesiosauromorph" and short-necked, large-headed "pliosauromorph" [25]. They were highly adapted to aquatic life, with four hydrofoil-like flippers, rigid trunks and possible tail fins [26, 27, 28]. Although they belong to diapsid Sauropterygia [26], plesiosaurs possessed many physiological features analogous to mammals (e.g., viviparity [29, 30], endotherm [31], high metabolic rates [32]).

Besides their great diversity in body plans, plesiosaurs also varied greatly in body size, from small taxon like *Thalassiodracon hawkinsi* that measures less than 2 meters [33], to gigantic thalassophoneans and elasmosaurs (>10 m [34, 35]). Numerous studies attempted to estimate the body sizes of different plesiosaur taxa, most of which focused on body length (e.g., [36, 34, 37, 38]). However, these estimations were carried out under different criteria and the results are often conflicting. In addition, linear measurements like body length may not be good proxies for plesiosaur size due to the high plasticity and diversity of their body proportions. On the other hand, attempts to estimate body masses of plesiosaurs are very rare, possibly precluded by lack of knowledge about the three-dimensional arrangement of their postcranial skeletons. Therefore, the body massses of many plesiosaur taxa remain mysterious to date.

Thanks to the burst of plesiosaur researches in the past two decades, our knowledge on their anatomy, physiology and evolutionary history has been greatly expanded. The discovery of some fossils with soft tissue imprints also sheds light on their body outlines. Now it is the suitable time to review previous studies and propose a set of criteria for plesiosaur body reconstruction.

The goal of this study is to: (1) perform a comprehensive review of relevant knowledge, criteria and discrepancies about plesiosaur reconstructions in previous studies; (2) propose a uniform set of methodology for body reconstruction and size estimation that can be applied to the whole Plesiosauria; (3) create multiple rigorous plesiosaur models and calculate their masses and surface areas; (4) use these models to generate scaling equations that enable quick body mass prediction from incomplete fossils. Results of this study would illuminate the great size disparity among plesiosaurs, offer tools for future studies and finally lead to better understanding of their evolutionary history.

1.1 Institutional abbreviations

NHMUK (formerly **BMNH**), Natural History Museum, London, U.K.; **SMU SMP**, Shuler Museum of Paleontology, Southern Methodist University, Dallas, U.S.A; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **MB**, Naturkundemuseum Berlin, Berlin, Germany; **CAMSM**, Sedgwick Museum of Geology, Cambridge, U.K.; **MCZ**, Museum of Comparative Zoology, Harvard University, USA; **FHSM**, Fort Hays State University, Sternberg Museum of Natural History, U.S.A.; **UANL**, Facultad de Ciencias de la Tierra, Universidad Autonóma de Nuevo León, Mexico. **MJACM**, Museo El Fósil, Vereda Monquirá, Colombia; **DMNH**, Denver Museum of Nature and Science, Denver, U.S.A. **UCMP**, Museum of Paleontology, University of California at Berkeley, Berkeley, California; **QM**, Queensland Museum, Queensland, Australia; **GPIT**, Geologisch-Paläontologisches Institut Tübingen, Tübingen, Germany; **PMO**, Palaeontology Museum, Natural History Museum, Oslo, Norway; **DORCM**, Dorset County Museum, Dorchester, U.K.; **USNM**, NationalMuseum of Natural History,Washington, D.C., U.S.A.; **MOZ**, Museo Profesor J. Olsacher, Zapala, Argentina; **OUMNH**, Oxford University Museum of Natural History, Oxford, U.K.; **ABGCH**, Abingdon County Hall Museum, Abingdon, U.K.; **YORYM**, Yorkshire Museum, York, U.K.; **MNA**, Museum of Northern Arizona, Flagstaff, U.S.A.; **MNHNL**, Muséum national d'histoire naturelle du Luxembourg, Luxembourg-ville, Luxembourg; **MChEIO**, Museum of Chuvash Natural Historical Society, Chuvashia, Russia; **TMP**, Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **KUVP**, Natural History Museum, University of Kansas, Lawrence, U.S.A.; **INAH**, Instituto Nacional de Antropología e Historia, Saltillo, Mexico; **YPM**, Yale Peabody Museum, New Haven, U.S.A.; **SGO.PV**, Museo Nacional de Historia Natural, Santiago, Chile;

1.2 Unit abbreviations

m, meter; **mm**, millimeter; **t**, tonne;

2 Preliminaries to plesiosaur reconstruction

Attempts to reconstruct plesiosaurs are often hampered by incomplete or fragmented nature of fossils, which might be crushed or distorted during taphonomic processes. Our knowledge on three-dimensional arrangement of plesiosaur postcranial skeletons is limited. Even in well-preserved, articulated fossils, skeletal elements necessary for reconstructions are sometimes obscured and thus unavailable (e.g., *Sachicasaurus vitae* [39]; *Meyerasaurus victor* [40]). Here I present a review of preliminary information relevant to plesiosaur reconstruction. If previous studies have already reviewed some certain areas related to

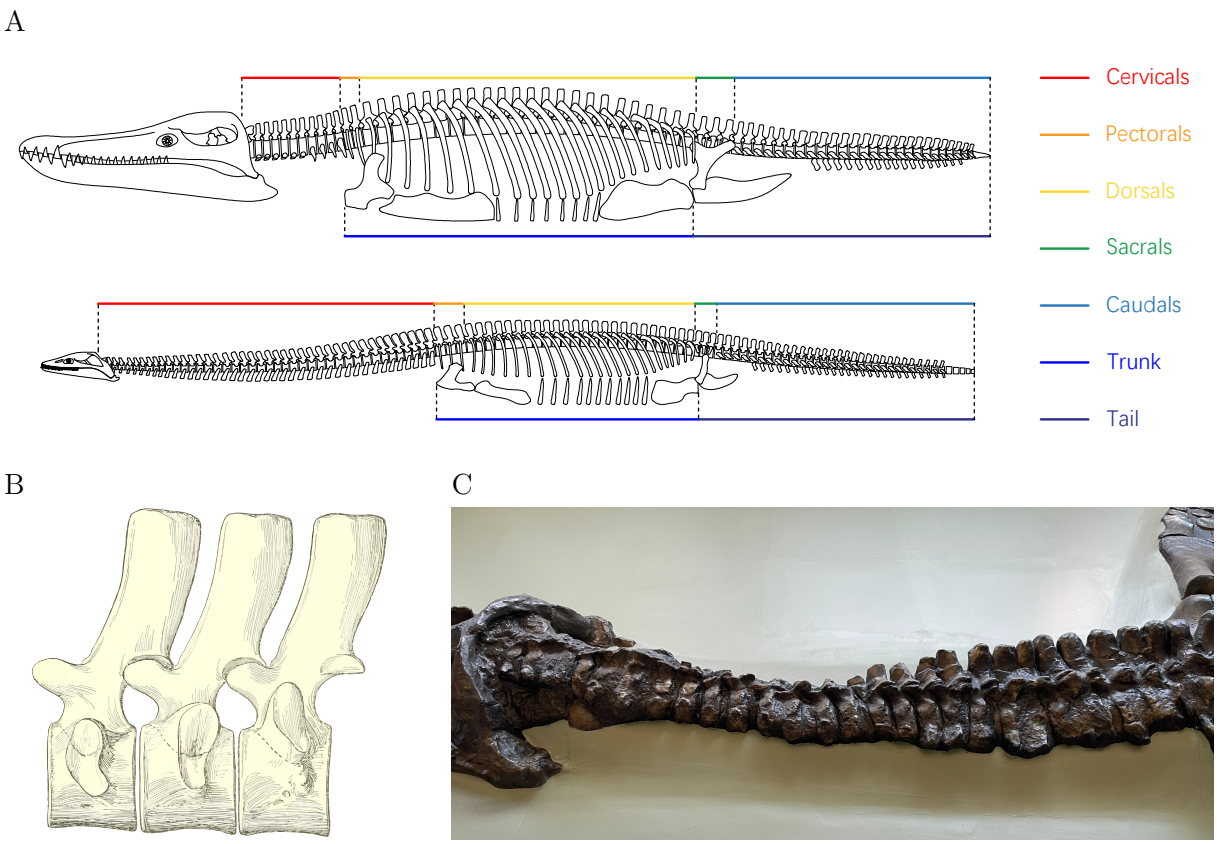

Figure 1: **A**, skeletal reconstructions of *Sachicasaurus vitae* and *Aristonectes quiriquinensis* (limbs removed), with different regions marked by colored lines. **B**, pectorals and the first dorsal of *Muraenosaurus leedsi*, vectored from Andrews ([41]: Fig. 52) using *Vector Magic*. **C**, photo of a cast of *Rhomaleosaurus cramptoni* (NHMUK PV R34) showing the intervertebral cartilages in the neck region, provided by Frederick Dakota.

this theme, I do not repeat all the details but attribute to them and add extra information if necessary.

2.1 Postcranial anatomy of plesiosaurs

Paul [42] emphasized that precise life reconstructions of vertebrates should be based on rigorously created skeletons. Therefore, a comprehensive understanding of skeletal elements and their patterns of three-dimensional arrangement is essential for plesiosaur body reconstructions.

2.1.1 Vertebral column

Traditionally, five types of vertebrae were recognized in plesiosaurs: cervicals, pectorals, dorsals, sacrals and caudals ([41, 43, 38, 34]; Fig. 1A). Pectoral vertebra is a special concept which is rarely used in other groups of vertebrates [35]. It was introduced by Seeley [44] and refers to the type of vertebrae with ribs partly attached to the centra and partly attached to the neural arches (see "pectoral shifts" in [45]; Fig. 1B). Sometimes it is tricky to identify the actual vertebral formulas in osteologically mature plesiosaurs because of fusion of neural arches to the centra [38]. Although widely used, the concept of

pectoral vertebrae is, however, not accepted by all researchers (e.g., [46, 47]). Some recent studies opposed this traditional concept by combining pectorals into cervicals or dorsals ([48, 49, 50]; [51, 52, 53]). Opinions on whether this terminology should be retained have not reached consensus [54], and inconsistent definitions have led to conflicting arguments in previous studies (e.g., 76 vs 75 cervicals in *Albertonectes vanderveldei* [46, 55]; 60 vs 62 cervicals in *Hydrotherosaurus alexandre* [36, 48]). Despite the discrepancy in previous studies, I retain the concept of pectoral vertebrae in this paper for unambiguous references.

In vertebrates, there exist cartilages separating adjacent vertebrae, and their forms vary across different clades [45]. Intervertebral cartilages are also present in plesiosaur fossils (Fig. 1C), but their type has rarely been discussed until recently. Synovial intervertebral articulation is typical in extant reptiles like crocodiles and lepidosaurs [56]. Wintrich et al [57] argued that conventionally hypothesized synovial joints would greatly reduce the mobility of necks in plesiosaurs because they possessed platycoelous centra rather than procoelous ones seen in crocodiles, so they proposed that plesiosaurs had intervertebral discs analogous to those of mammals. In a later study, Wintrich et al [58] once again suggested the presence of intervertebral discs in eosauropterygians (an extinct clade including Plesiosauria [59]) and non-avian dinosaurs. On the other hand, some researchers argued that central scars on articulated faces of plesiosaur vertebral corpora indicate synovial joints (Eberhard Frey, pers. comm, 2022). Since this problem is still in debate, I avoid designating specific type of vertebral joints but use the terminologies "intervertebral cartilage" or "intervertebral distance" in this paper.

Intervertebral cartilages are important components of body length, and neglecting them would lead to a significant underestimation of body size [35]. Some previous studies measured intervertebral distances from articulated fossils, most of which focused on intercervical cartilages. The sizes of intercervical cartilages vary greatly depending on position, taxonomic status and how the neck was arranged during taphonomic processes [54]. Andrews [60] described the intervertebral cartilages in the cervical and thoracic regions of *Leptocleidus superstes* NHMUK PV R4828, which is about 5 mm each [61]. In *Libonectes morgani* SMU SMP 69120, the intercervical cartilage is 7 mm by average [62]. The intercervical cartilages in *Nichollssaura borealis* range from 7 to 16 mm [63]. Some studies designated intercervical distances when handling disarticulated cervical series (e.g., 1-3 mm in [64, 57], 2 mm in [65, 66]). A collection of intercervical distances in different plesiosaur taxa is shown in Table 1. It is notable that intervertebral distances increase with size of the animal (e.g., 11.54 mm by average in ∼5 m *Brachauchenius lucasi* [35] vs 18.25 mm in ∼10 m *Sachicasaurus vitae*, [39]: Fig. 5). Hence Troelsen [54] argued that it is better to use ratios rather than absolute lengths. In addition, plesiosaurs with fewer cervicals tend to possess proportionally larger intercervical distances, which probably worked as compensations for reduction in cervical number to increase neck mobility [57]. In the pectoral, dorsal and sacral regions, the ratios of intervertebral cartilages to adjacent vertebrae seem to be constant (∼10 %) in a broad range of plesiosaur taxa (e.g., *Brachachenius lucasi* [35]; *Rhomaleosaurus thorntoni*, [67]: Plate 13-20; *Elasmosaurus platyurus* and *Seeleyosaurus guilelmiimperatoris*, [55]: Fig. 3). This is possibly because the rib cages in plesiosaurs were quite stiff in life so that intervertebral cartilages did not undertake the task to adjust vertebral mobility as in the cervical region [26].

Many previous studies stated that tails of plesiosaurs are too short to be used for propul-

Table 1: Collection of intercervical distances (either measured or assumed) from previous studies.

Taxon	Clade	Description	Ref
Leptocleidus superstes	Leptocleididae	intercervical distance about 5 mm each;	[61]
Nichollssaura borealis	Leptocleididae	intercervical distances ranging from 7∼16 mm;	[54]
Libonectes morgani	Elasmosauridae	neck length 5618 mm, including 421 mm intercervical cartilages;	[62]
Hydrotherosaurus alexandrae	Elasmosauridae	about 1 cm between anterior cervical spines, and posterior cervicals almost touch;	[36]
Elasmosaurus platyurus	Elasmosauridae	intervertebral distances in the middle cervical region larger than 1 cm;	[34]
Kawanectes lafquenianum	Elasmosauridae	(assumed) intervertebral distance 2 mm each;	[66]
Aristonectine indet	Elasmosauridae	(assumed) intervertebral distance 2 mm each;	[65]
Multiple elasmosaurids	Elasmosauridae	(assumed) intercervical distance 1∼3 mm each;	[64]
Cryptoclidus eurymerus	Cryproclididae	15%∼26% of anterior cervical lengths;	[68]
Cryptoclidus eurymerus	Cryproclididae	(assumed) intercervical distance 1∼3 mm each;	[57]
Muraenosaurus leedsi	Cryproclididae	4%∼19% of anterior cervical lengths;	[68]
Ophthalmothule cryostea	Cryproclididae	intercervical distances 2.7∼5.8 mm (5.5%∼15.5% of cervical lengths, 9.3% by average);	[54]
Multiple plesiosauroids	Plesiosauroidea	(assumed) intercervical distance around 1 cm each;	[69]
Trinacromerum bentonianum	Polycotylidae	intervertebral distances about 3∼6 mm;	[70]
Thalassiodracon hawkinsi	Pliosauridae	intercervical distances 0.8∼3.4 mm (4%∼19% of cervical lengths, 10.1% by average);	[54]
Brachauchenius lucasi	Pliosauridae	intercervical distances 9∼18 mm (24.8% of cervical lengths by average);	[35]

sion and can only function as tools for direction control, stabilization or streamlining [71, 1, 72, 73, 47]. However, this cognition may be biased due to the poor preservation of tails in many plesiosaur fossils [74, 75, 50, 22]. In some early Jurassic plesiosaurs, the tails were almost equal in length with the trunks (e.g., *Hauffiosaurus tomistomimus* [53], *Atychodracon megacephalus* [67], *Thalassiodracon hawkinsi* [76], Plesiosauroidea indet SMNS 51945 [77]; see the next section for definitions of trunk and tail). Such a condition continued into late Jurassic and Cretaceous: thalassophoneans, cryptoclidids and elasmosaurids also possessed long tails comparative in length with their trunks (e.g., *Peloneustes philarchus* [43], *Cryptoclidus eurymerus* [38], *Albertonectes vanderveldei* [46]). But in polycotylids, the tails were much shortened, exemplified by *Dolichorhynchops osborni* and *Mauriciosaurus fernandezi* [78, 47].

Owen [79] studied the tails of some plesiosaur species from Liassic. He noticed that the intercaudal distances in *Plesiosaurs dolichodeirus* are large, similar to the condition in the spine of fishes. In *Microcleidus homalospondylus*, the tall caudal centra and corresponding spines are indicative to a large amount of muscles attached to the tail and greater mobility than the neck [79]. Evidence of tail flexibility is also present in the fossils of rhomaleosaurids, cryptoclidids and elasmosaurids, all of which possess large intercaudal distances [80, 81, 27, 82, 83, 84]. Due to the flexibility of tails in plesiosaurs, Sennikov [85] proposed that they played important roles in propulsion, diving and predation. On the other hand, the intercaudal cartilages are extremely narrow in *Mauriciosaurus* [47], which indicate minor flexibility and may represent a synapomorphy of polycotylids (Eberhard Frey, pers. comm, 2022).

Many plesiosaur fossils are dorsalventrally crushed, hence the curvatures of their vertebral columns in life are unknown. Dating back to the 19th and 20th centuries, plesiosaurs were often reconstructed as animals patrolling around the water surface with swan-like or snake-like necks (Fig. 2AB). However, recent studies have demonstrated that such a bending of the neck is impossible for plesiosaurs [64, 86]. This posture never appears in articulated fossils either. In some early reconstructions, plesiosaurs have arched dorsal regions ("hump" in [87]), exemplified by the classic reconstructions of plesiosaurs from Oxford Clay Formation by Andrews ([41, 43]; Fig. 2D, Fig. 3A). The pliosaur reconstruction by Newman and Tarlo also possesses a humped back ([88]; Fig. 3F). Arched backs can still be seen in some modern reconstructions (e.g., Fig. 2F). On the other hand, the vertebral columns in other reconstructions are straight or gently arched (e.g., Fig. 2CG, Fig. 3E). To date whether plesiosaurs had humped backs or not is still in debate (Richard Forrest, pers. comm, 2021; Leslie Noè, pers. comm, 2022). Robinson [89] argued that an arched vertebral column, analogous to a bow, could function as a transmitter of propulsive forces through the trunk. But this is not agreed by Smiths and Benson, who reviewed previous reconstructions and listed some well-preserved fossils as counterexamples against a humped back [87]. Richards [90] used wedging angles and face angles of plesiosaur dorsal vertebrae to reconstruct the columns. In Richards' reconstructions, the spines of *Tatenectes* and *Cryptoclidus* are gently curved as proposed by Smiths and Benson [87], but *Muraenosaurus* has a humped back, similar to the reconstruction produced by Andrews [41]. Therefore, it is possible that spinal curvature may vary across plesiosaur taxa and there doesn't exist a uniform rule that the back must be humped or not.

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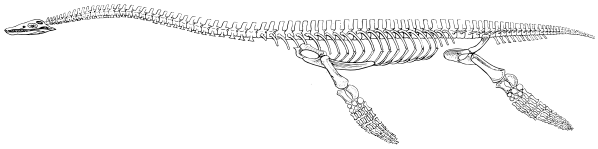

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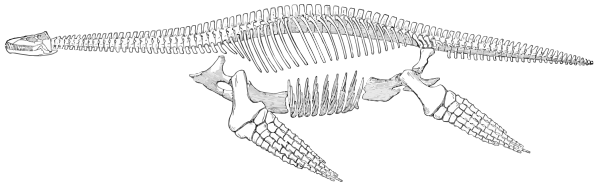

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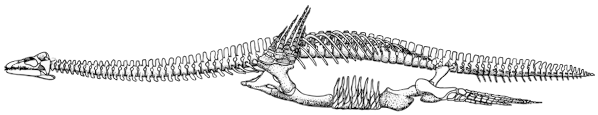

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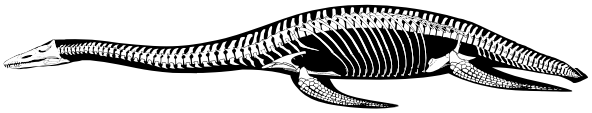

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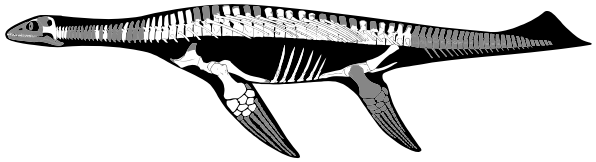

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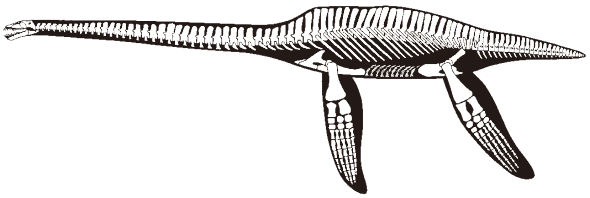

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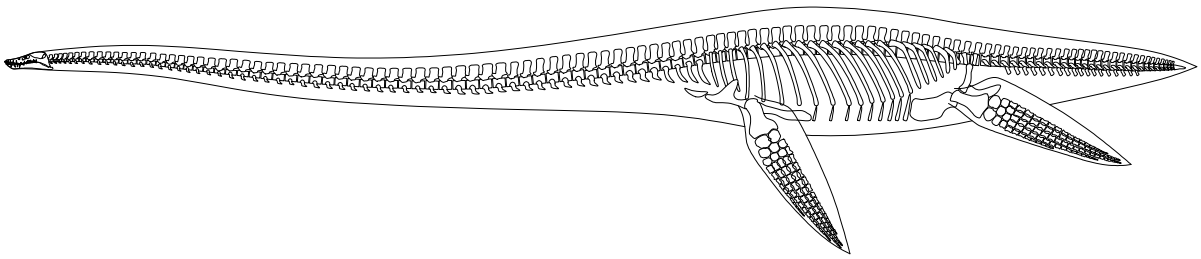

Figure 2 (*previous page*): Body reconstructions of long-necked plesiosaurs from different times. **A**, 1840 painting *The Sea-Dragons as They Lived*, from [91]. **B**, 1959 painting of an elasmosaur fighing against a mosasaur, from [92]. **C**, *Plesiosaurus dolichodeirus* (1824), from [93]. **D**, *Cryptoclidus eurymerus* (1910), from [41]. **E**, *Cryptoclidus eurymerus* (1981), from [38]. **F**, *Brancasaurus brancai* (2016), from [94]. **G**, *Tatenectes laramiensis* (2010), from [81]. **H**, *Microcleidus homalospondylus* (2022), from [95]. **I**, *Styxosaurus*, from this study. Figure C-H were vectored using *Vector Magic*.

2.1.2 Rib cage

The rib cages of plesiosaurs are immobile structures, which are stiffened by enlarged girdles articulated by rows of gastralia ([26]; Fig. 4A). The rib cage consists of the dorsal basket (vertebral column and ribs) and ventral basket (girdle elements and gastralia) [89]. The small size of ilium and the dorsal blade of scapula suggests that the ventral basket was loosely attached to the dorsal basket in life and could be removed as a whole structure [89, 99, 100].

All dorsal ribs in plesiosaurs are single-headed, attached to the transverse processes of the neural arches [41, 101, 38]. Therefore, the orientation of each rib can be determined from the shape of corresponding transverse process [102, 90]. Richards [90] proposed two slant angles which can be measured directly from transverse processes. They are adopted in this study (Fig. 4B). The angle between rib and vertical plane from side view is defined as "angle α" here, and the angle between rib and vertical plane from dorsal view is defined as "angle β". The sizes of slant angles vary greatly across plesiosaur species. In *Cryptoclidus eurymerus*, the maximum angle α is about 50 ° [90] while in *Dolichorhynchops herschelensis* it is only about 10 ° ([103]: Fig. 7). Judging from well-preserved plesiosaur fossils, the sizes and slant angles of transverse processes shift gradually. The transverse processes often increase in size till middle of the dorsal region and become shortened afterwards [41, 38]. Angle α also increases gradually from 0 ° in anterior dorsals to maximum in middle of the dorsal region, and keeps almost constant in the posterior half of dorsal series but decreases to 0 ° again rapidly when approaching sacral region (Fig. 4C). On the other hand, angle β increases monotonically from 0 ° to maximum, and remains constant with no recovery. Such an arrangement of rib orientation, which seems to be widespread among plesiosaurs, was described by previous researchers or can be observed from well-preserved fossils (e.g., *Cryptoclidus eurymerus* [38]; *Muraenosaurus leedsi* [41]; *Tatenectes laramiensis* [102]; *Rhomaleosaurus thorntoni* [87]; *Attenborosaurus conybeari* [50]; *Fluvionectes sloanae* [104]; *Colymbosaurus svalbardensis* [105]; *Avalonnectes arturi*, pers. comm with Frederick Dakota, 2023). The ribs also change in shape and size throughout the dorsal region. They typically increase in length gradually in anterior half of the dorsal region, then become shorter and straighter in posterior half (e.g., *Cryptoclidus eurymerus* [38]; *Monquirasaurus boyacensis* [74]; *Attenborosaurus conybeari* [50]; *Dolichorhynchops osborni* [78]; *Brancasaurus brancai* [94]).

The ventral basket consists of pectoral girdle, pelvic girdle and gatralia connecting them. The pectoral girdle contains interclavicle, clavicles, scapulae and coracoids, and the pelvic girdle contains pubes, ischia and illia [41, 43]. Fusion of interclavicle and clavicles can be observed in many osteologically mature plesiosauroids and rhomaleosaurids

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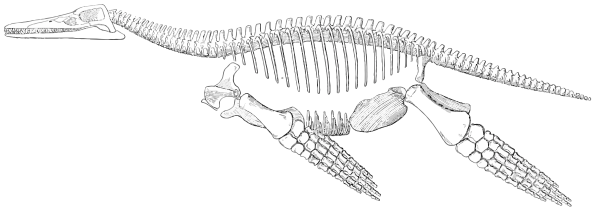

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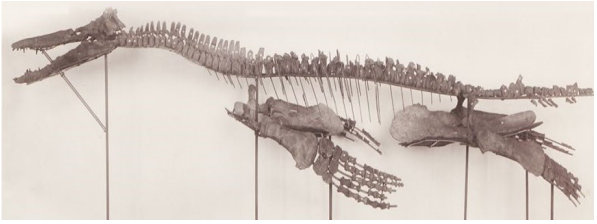

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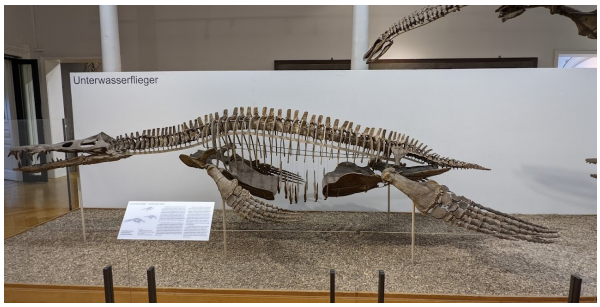

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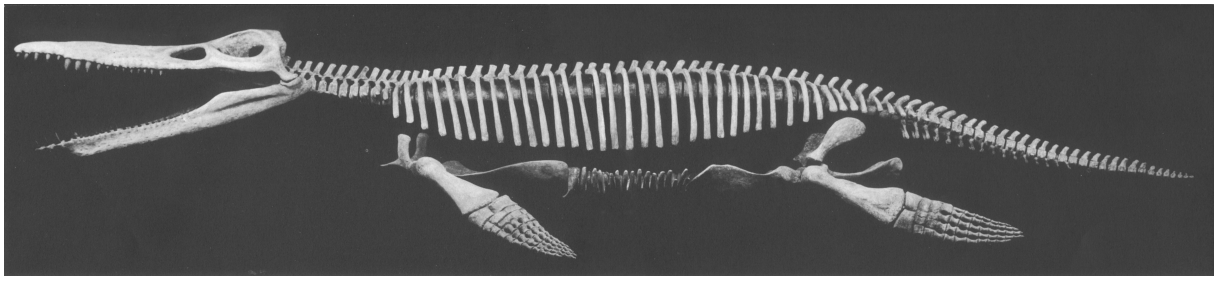

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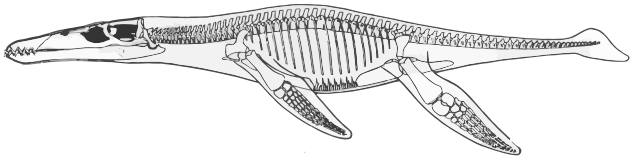

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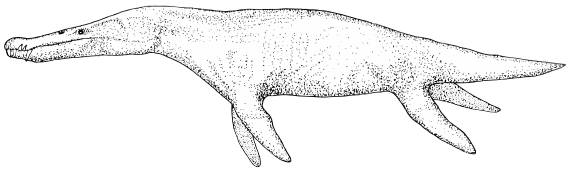

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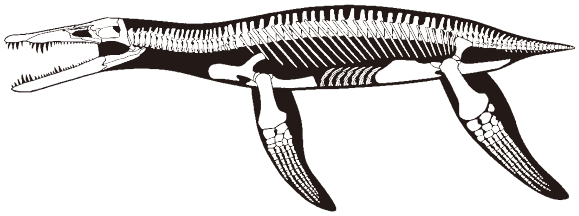

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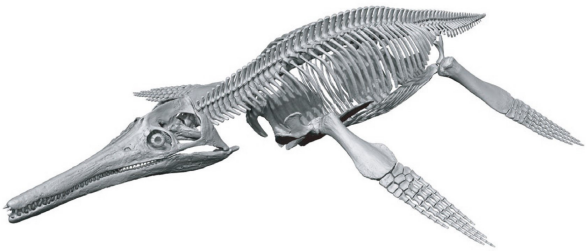

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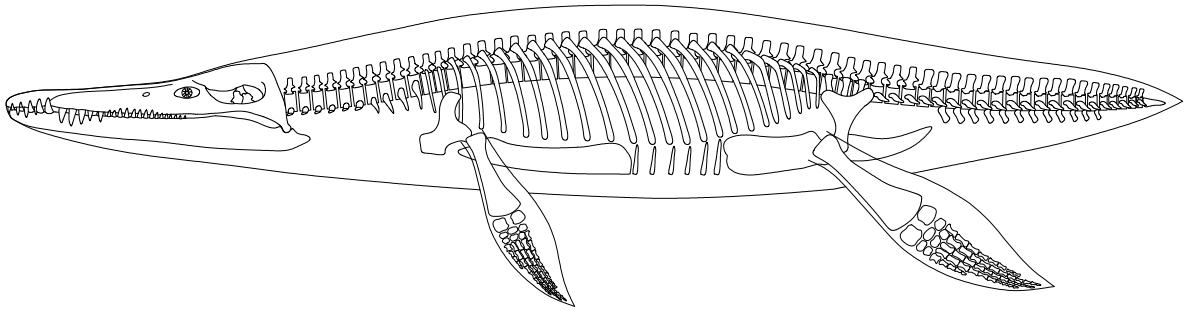

Figure 3 (*previous page*): Body reconstructions of short-necked plesiosaurs from different times. **A**, *Peloneustes philarchus* (1913), from [43]. **B**, historical mount of *Peloneustes philarchus* (GPIT/RE/3182, photographed in 1920), from [96]. **C**, mount of *Liopleurodon ferox*, photo provided by Anna Krahl. **D**, restoration of *Kronosaurus/Eiectus* (1924), from [97]. **E**, mount of *Kronosaurus/Eiectus* (1956), from [37]. **F**, "a typical giant pliosaur" (1967), from [88]. **G**, *Monquirasaurus boyacensis* (1992), from [98]. **H**, *Liopleurodon ferox* (2022), from [95]. **I**, *Luskhan itilensis* (2023), from [75]. **J**, *Kronosaurus/Eiectus*, from this study. Figure A, F-H were vectored using *Vector Magic*.

[38, 106, 40, 107, 104], but they are not present in some elasmosaurids (e.g., "*Mauisaurus haasti*" [108]; *Wapuskanectes betsynichollsae* [52]; *Aristonectes quiriquinensis* [109]). In addition, interclavicles are generally abesent in the fossils of thalassophonean pliosaurs [110]. An asymmetrical, triangular structure is present in *Peloneustes philarchus* and was identified as an interclavicle [43, 111]. However, it has been reinterpreted as a clavicle by Ketchum and Benson [112], but the re-evaluation is uncertain in the current stage [113]. The coracoids, pubes and ischia of plesiosaurs are plates of bones. Two symmetric elements of these two bones meet with each other in the sagittal plane, forming median symphyses and intersection angles. Each of them forms a V-shape with corresponding symmetric element [43]. The sizes of intersection angles vary across species. In the reconstruction of *Hydrotherosaurus alexandre* by Welles [36], the intersection angles between coracoids and pubes are around 150° and 130° respectively. Andrews [43] stated the angle between the two coracoids of *Peloneustes philarchus* is about 90°. Williston [78] reported a 125° angle between the pubes of *Dolichorhynchops osborni*. From side views, the positions where girdle elements meet and articulate are V-shaped embayments for limb insertion (glenoid in pectoral girdle and acetabulum in pelvic girdle) [41, 43].

Each row of gastralia in plesiosaurs often contains three types of elements: a median structure uniting bilaterally symmetric ossicles [38, 104], while evidence for the existence of medial elements is absent in some species (e.g., *Aristonectes quiriquinensis* [109]). The number of rows of gastralia varies across species, ranging from 6 to 12 [76]. They were united with each other and with the ribs by ligaments and cartilages in life [71, 89].

2.1.3 Limbs

Plesiosaurs are secondarily aquatic tetrapods, possessing four hydrofoil-like flippers [71, 28, 114]. The flippers are significant components of body mass and surface area due to their large sizes, thus precise limb reconstructions are essential for plesiosaur size estimation [4]. Skeletal arrangement of plesiosaur limbs is homologous to those of other tetrapods, each of which contains a propodial, epipodials, mesopodials, metapodials, and phalanges [115, 116, 117]. They also display hyperphalangy, indicative of smooth bending and additional twisting, which were hydrodynamically advantageous during swimming [118, 28].

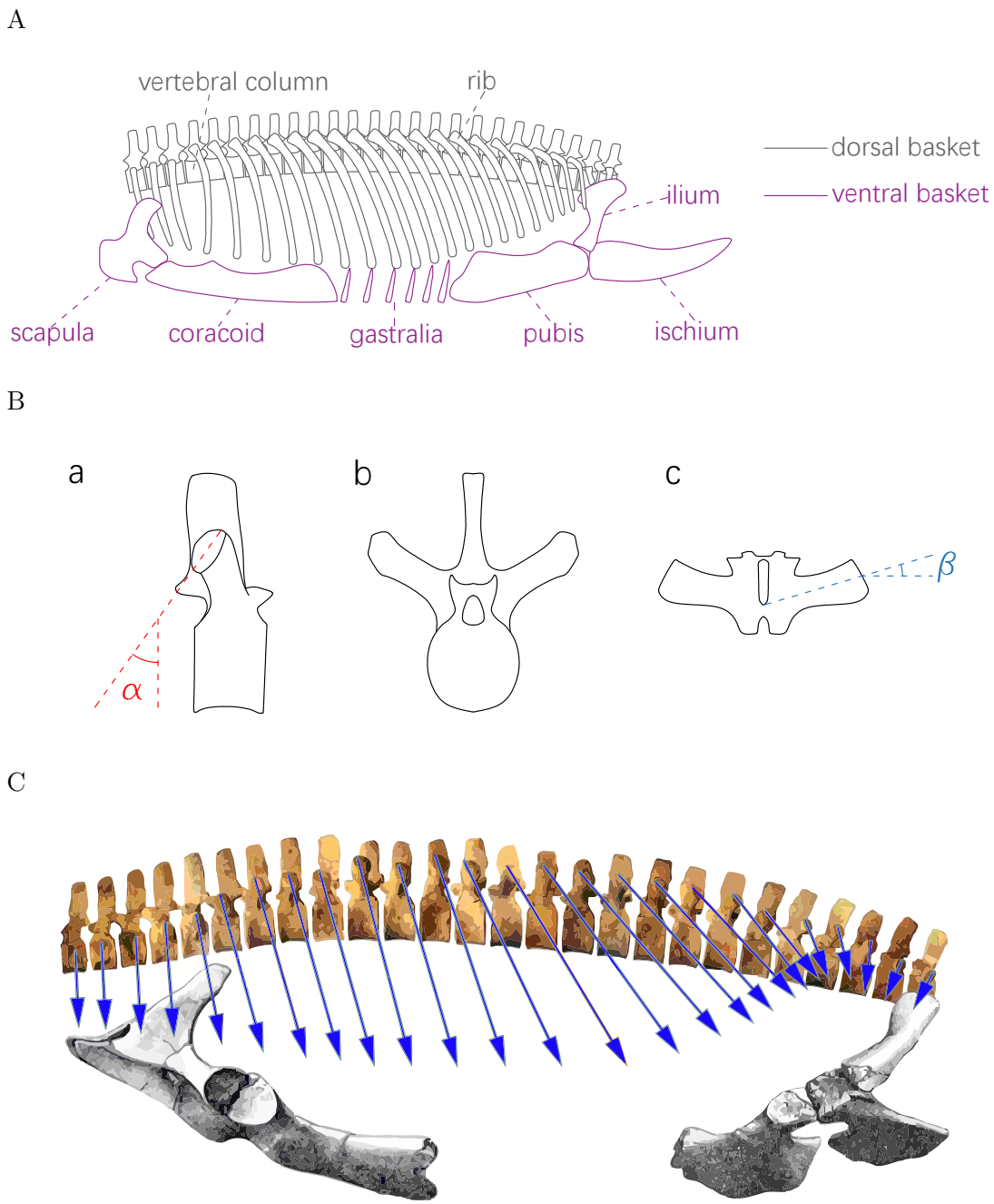

Figure 4: **A**, rib cage of *Peloneustes philarchus*. **B**, different views of plesiosaur dorsal vertebra, showing two slant angles: **a**, right side view; **b**, front view; **c**, dorsal view. **C**, rib cage of *Cryptoclidus eurymerus*, with blue arrows representing rib orientations in side view, reproduced from [90].

2.2 Soft tissue reconstruction

2.2.1 Plesiosaur fossils with soft tissues

Some plesiosaur fossils are preserved with imprints of soft tissues. The earliest reports of soft tissue outlines in plesiosaur fossils date back to the 19th century. Sollas [50] noticed possible soft tissue preservation in the holotype of *Attenborosaurus conybeari*, which was unfortunately destroyed in World War II [77]. *Seeleyosaurus guilelmiimperatoris*

MB.R.1992 has soft tissue outlines around its tail and right forelimb ([119]; Fig. 5A). This fossil is, however, currently covered by paint, which obscures the soft tissue profiles [80]. There were 2 plesiosaur fossils with soft tissue imprints described in the 20th century: the holotype of *Microleidus brachypterygius* and a single flipper described by Watson [120, 121], but their authenticity was questioned by previous researchers [115, 117]. In general, all plesiosaur fossils with soft tissue preservation described in the 19th and 20th centuries are currently unavailable or of doubtful reliability.

Vincent et al [77] described SMNS 51945, a long-necked plesiosaur fossil with soft tissue preservation around its vertebral column and hindlimbs. The imprints around the hindlimbs in SMNS 51945 suggest that soft tissues expand the flippers to a proportionally greater extent than in those of *Microleidus brachypterygius* [77]. Although it partially illuminates the body outlines of plesiosaurs in life, SMNS 51945 offers very limited reference for quantitative soft tissue reconstruction of plesiosaur trunks. It should be noted that the profile around the body ([77]: Fig. 1) is an artifact created during the preparation of this fossil rather naturally preserved outline (Peggy Vincent, pers. comm, 2022).

Frey et al [47] described *Mauriciosaurus fernandezi*, a polycotylid plesiosaur with extensive soft tissues around its body (Fig. 5B). Although the thickness of soft tissues might be slightly exaggerated during taphonomic processes, this specimen is the best reference for plesiosaur soft tissue reconstruction to date. The soft tissue imprints indicate that the body outline of *M. fernandezi* in life was streamlined, similar to that of a leatherback turtle (*Dermochelys coriacea*) [47]. It is notable that the rib cage of *M. fernandezi* is collapsed, with ribs detached from the vertebral column ([47]: Fig. 8). Therefore, a precise reconstruction of the rib cage is required before quantifying the amount of soft tissues. There are also soft tissues in the limb regions of this fossil, but outlines anterior to the flippers are not preserved.

2.2.2 Head and neck

No study to my knowledge quantitatively discussed the amount of soft tissues in the head regions of plesiosaurs. Several researchers described boss-like structures on ventral symphyses of some elasmosaurid mandibles [125, 106, 126]. This kind of structure has been interpreted as attaching site of geniohyoid muscle [109]. The morphology of ventral boss in *Aristonectes quiriquinensis* indicates a loose mouth floor [127], but the soft tissue outline of its skull is unknown. Due to the lack of direct evidence for cranial soft tissue outline, modern aquatic tetrapods are needed as references. Aquatic mammals possess thick fat tissue around their skulls. Odontocetes (toothed whales) possess melons, which function as echolocation organs consisting of fat and connective tissue [128]. Mysticetes (baleen whales) also possess thick soft tissues around their skulls and fatty structures for sound transmition [129]. All pinnipeds possess well-developed cranialfacial soft tissues and suction feeders have larger masseter muscles [130]. In modern aquatic or semiaquatic reptiles like sea turtles and crocodiles, however, there is little fat tissue around their skulls [131, 132]. It has been proved that the limited amount of soft tissues around the skull of leatherback turtle (*Dermochelys coriacea*) are sufficient to minimize heat loss [133].

The fossil of *Mauriciosaurus fernandezi* reveals that the necks of plesiosaurs were thicker in life than traditionally reconstructed [54]. Many modern aquatic tetrapods possess thick necks. The neck outlines of cetaceans and pinnipeds are smooth curves connecting their

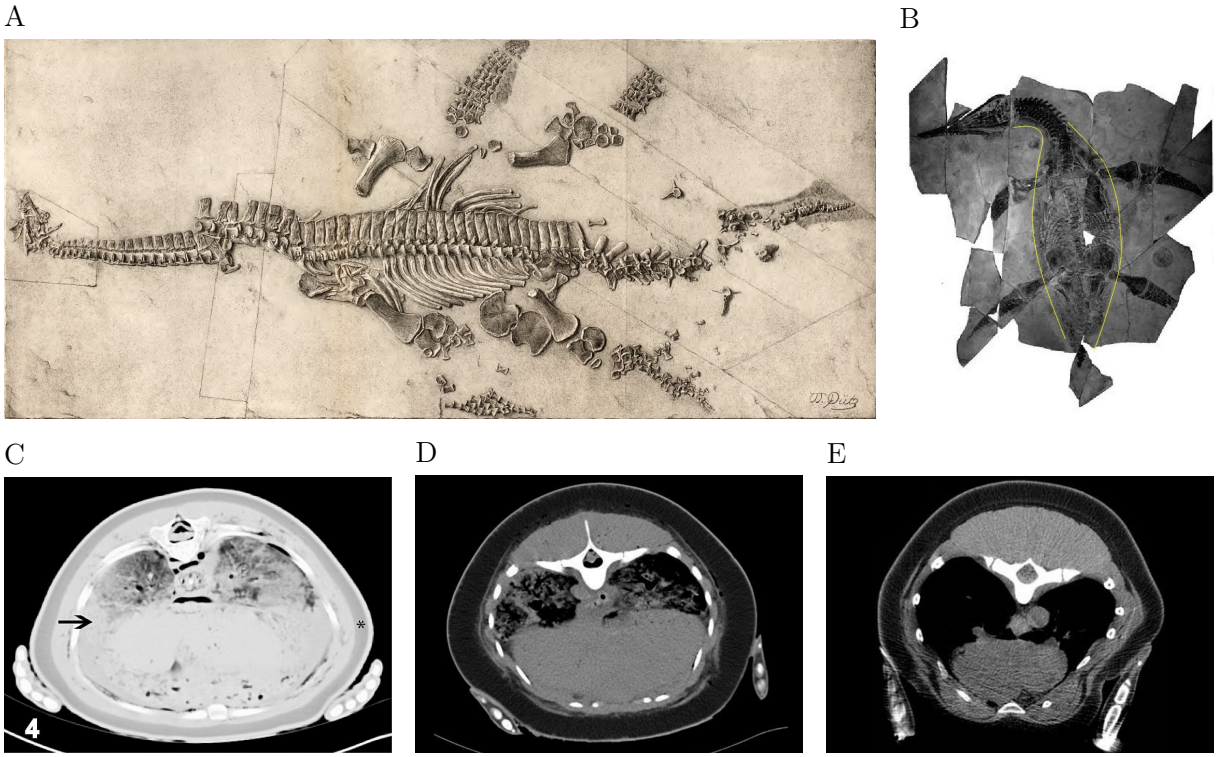

Figure 5: Plesiosaur fossils with soft tissue preservation and thoracic CT scans of modern marine mammals. **A**, illustration of the holotype of *Seeleyosaurus guilelmiimperatoris*, from [119]. **B**, the holotype of *Mauriciosaurus fernandezi*, with yellow curves representing preserved body outline, reproduced from [47]. **C**, the thoracic cross-section of a harp seal (*Pagophilus groenlandicus*), from [122]. **D**, the thoracic cross-section of a harbor porpoise (*Phocoena phocoena*), from [123]. **E**, the thoracic cross-section of a bottlenose dolphin (*Tursiops truncatus*), from [124].

heads and rib cages. In leatherback turtle (*Dermochelys coriacea*), the cervical vertebrae are also covered by thick fat [133]. It is likely that plesiosaurs possessed thick necks as well to prevent heat loss in high latitude regions or deepwater environments [134, 135]. Having thick necks could also give plesiosaurs hydrodynamic advantages, which might compensate for energy consumption in growing and nurturing them [136]. There exist large amounts of muscles in the necks and temporal regions of crocodiles, enabling them to produce great force during predation [137]. Some thalassophonean pliosaurs were also macrophagous, thus they might possess well-developed muscles in their necks like crocodiles [138, 35, 139].

2.2.3 Rib cage

Previous studies seldom discussed the amount of soft tissues around the rib cages of plesiosaurs, possibly due to the late discovery of *Mauriciosaurus fernandezi*. In most published reconstructions, the body outlines are not provided or drawn close to the skeletons (e.g., Fig. 2C-H, Fig. 3FH). To my knowledge, only the recent study carried out by Gutarra et al in 2022 [4] quantitatively restored the amount of soft tissues in the trunk region according to *M. fernandezi*. In spite of the marvelous preservation of *M. fernandezi*, many aspects of soft tissue arrangement in plesiosaurs remain unclear (e.g., the amount of soft tissues in dorsalventral sides of the trunk). This leaves room for interference, which can be based on plesiosaur physiology, muslce reconstructions and comparison with modern

aquatic tetrapods.

Plesiosaurs were physiologically similar to modern aquatic mammals, and have been termed as "long-necked dolphins" in recent studies (e.g., [136]). They were endothermic animals, having metabolic rates within the range of avians [32]. Judging from oxygen isotopes, the body temperatures of them ranged from 33 °C to 37 °C [31]. Evidence for decompression syndrome is present in many plesiosaur fossils, hence some species might adopt deep-diving habits [140]. Two plesiosaur fossils were found as evidence for viviparity: *Polycotylus latipinnis* [29] and *Abyssosaurus nataliae* [30]. Given the presence of viviparity in other eosauropterygians like nothosaurs and pachypleurosaurs [141], and the distinct relationship between *P. latipinnis* and *A. nataliae*, it is possible that all plesiosaurs gave birth to infants. Compared with maternal adults, the fetuses were proportionally large, indicative of a k-selected lifestyle [29]. The fossil of *M. fernandezi* also demonstrates that at least polycotylids, but possibly all plesiosaurs, possessed extensive soft tissues around their rib cages [47]. Due to their similarity in physiology, the soft tissue anatomy of modern endothermic aquatic tetrapods may shed light on plesiosaur reconstructions.

Modern marine mammals like cetaceans and pinnipeds possess thick blubber beneath the skin, which play the roles of thermal barrier, energy storage, hydrodynamic streamlining and buoyancy regulation [142, 143, 144, 145]. The function of blubber as thermal barrier is essential for them to sustain body temperature because of the high thermal conductivity of water [146]. Plesiosaurs, on the other hand, seemed to prefer high latitude and cold water environments. Many species are known to inhabit in or seasonally migrate to polar regions [134, 147, 148, 149, 150]. Without fur or hair, plesiosaurs were also likely to possess thick fat tissue to prevent heat loss. This is supported by the abundant soft tissues in *Mauriciosaurus fernandezi*, which was, however, a species dwelling in warm water environment [151, 47]. Cetaceans from high latitude regions generally tend to possess thicker blubber than those from warmer seas [152, 153]. It is possible that plesiosaurs also follow this rule, but a quantitative study is not applicable in the current stage.

Besides a geographic view, musculoskeletal and kinematic properties of plesiosaurs should also be taken into consideration. The rib cages of modern marine tetrapods are surrounded by muscles and ligaments (known as "core" in relevant studies, see [154] for example), outside of which are fat (blubber) and skin. The thoracic cross-sections in aquatic mammals are usually similar in shape to corresponding core profiles formed by muscles ([122, 124, 123]; Fig. 5CDE), thus muscle arrangement of plesiosaurs is also needed to reconstruct their body shapes. The attempts for muscular reconstruction of plesiosaurs have lasted for a century, most of which focused on the myological mechanism of their limbs and girdles. The earliest study on this theme dates back to 1924, when Watson [155] reconstructed the muscles attached to pectoral girdles and humeri of some long-necked plesiosaurs. Tarlo studied the forelimb muscles of *Pliosaurus* cf. *kevani* CAMSM J. 35990, of which the "scapula" turned out to be an ilium later [156, 157]. Robinson [71] reconstructed the muscular system of *Cryptoclidus eurymerus* and proposed that the locomotory strategy of plesiosaurs was underwater flight, analogous to the method applied by modern penguins and sea turtles. Carpenter et al [158] reconstructed the girdle musculature of *Dolichorhynchops*, and Araújo and Correia [159] applied a phylogenetic bracket method to infer pectoral musculature in plesiosaurs. The latest study is the new muscular reconstruction of *C. eurymerus* girdles by Krahl and Witzel [160], in which a review and comparison of muscle

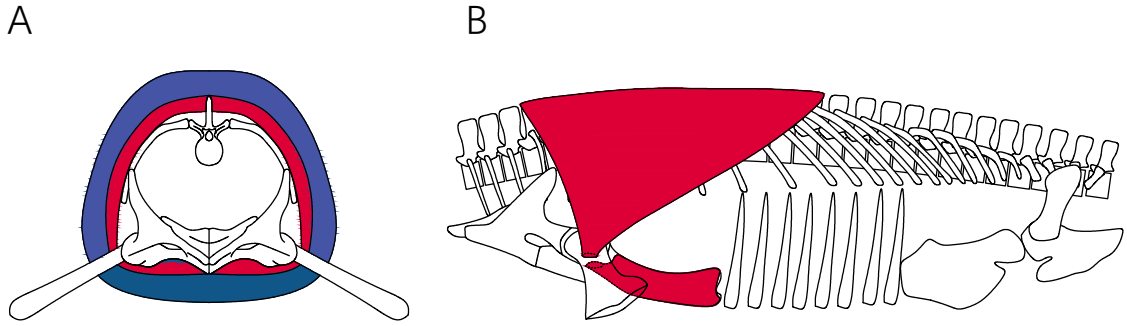

Figure 6: Illustration showing the main elevator (*m. latissimus dorsi*) and main depressor (*m. pectoralis*) of plesiosaur (*Cryptpclidus eurymerus*) forelimbs, reconstructed based on conclusions from [158, 159, 160] and marked in red. **A**, front view of rib cage, with fat tissue and skin colored in blue. **B**, side view of rib cage.

restoration criteria can be found. Figure 6 shows the main elevator and depressor musles of plesiosaur forlimbs, based on recent myological studies. Although the muscle restorations from different studies are somewhat inconsistent, a conclusion can be drawn that well-developed locomotory muscles were attached to the ventral sides of plesiosaur girdles in life. Thus thick soft tissues beneath the rib cage should be added during reconstruction.

Currently there is a consensus that plesiosaurs applied a lift-based appendicular swimming mode, namely underwater flight [73, 161, 116, 162]. In spite of their similarity in locomotory style, types of muscle arrangement in underwater fliers are distinct from each other. Sea turtles (except leatherback turtle *Dermochelys coriacea* [163]) are ectothermic animals, having low metabolic rates and slow cruising speeds [164, 165]. Their major forelimb muscles for locomotion, which gather at their pectoral girdles and plastrons without attachment to the vertebrae, are distinct in arrangement to those of plesiosaurs [132]. The presence of carapace and their preference for a mixed diet including vegetation and benthic animals also suggest that they are not suitable references for soft tissue reconstructions of plesiosaur rib cages [166, 167]. Penguins have high metabolic rates and are active predators [168, 169]. The main elevator and depressor muscles of their wings are, however, on the ventral side of the pectoral girdle, similar to those of flying avians [170]. Such muscle arrangement is quite distinct from that in plesiosaurs, of which the main elevators of limbs originate from dorsal side of their thoraxes ([160]; Fig. 6). Some pinnipeds like otariids also adopt underwater flight [171, 172]. The extension range of their glenohumeral joints is limited, leading to asymmetric strokes during swimming: the downstroke is propulsive, and the upstroke is a passive recovery [173, 174]. This requires the limbs to possess large range of motion anteroposteriorly, which can not be achieved by plesiosaurs judging from their girdle anatomy [158]. Therefore the stroke style applied by plesiosaurs, which predominantly consisted of dorsalventral motions, was different from that applied by pinnipeds [115].

In cetaceans, epaxial swimming muscle *m. longissimus dorsi* runs along the postcranial skeleton and surrounds the neural arches [175]. The main elevator of plesiosaur forelimb, *m. latissimus dorsi*, originated from the vertebral column and ranged from the 1st to 12th dorsal vertebrae [160]. The tall neural arches and long transverse processes of

plesiosaurs resemble those of cetaceans, suggesting that they also possessed well-developed epaxial muscles for flipper elevation. Therefore, thick soft tissues should also be added to dorsal side of the trunk when reconstructing a plesiosaur.

2.2.4 Tail

The tail of *Mauriciosaurus fernandezi* in life contained contour fat, which extended the trunk outline to the tail without constriction, making a streamlined body [47]. It is possible that counter fat also existed in the tails of other plesiosaurs for hydrodynamic advantage, and caudal vertebral anatomy suggests larger amount of muscles and greater tail mobility in clades other than polycotylids [79]. The last several caudals in many plesiosaur fossils are fused to form pygostyle-like structures. It is phylogeneticly widespread among plesiosaurs, and a summary of plesiosaur taxa with fused terminal caudals has been carried out by Clark et al [176]. This structure has been intepreted to indicate a tail fin [85]. Many researchers mentioned the possible presence of tail fins in plesiosaurs based on caudal morphologies or soft tissue imprints (e.g., [119, 88, 81, 80, 85]). But whether their tail fins were vertically or horizontally oriented is still in debate ([27, 80]; [127, 85]), and their shapes are not known to date. In addition, it remains unclear whether the tail fins (if existed) of different plesiosaur clades were homologous structures or evolved independently for multiple times.

2.2.5 Flipper profile

Various methods and criteria have been used to reconstruct the flipper outlines of plesiosaurs. Bakker [177] reconstructed flippers with outlines close to the bones, but this is not realistic due to the presence of soft tissue imprints in fossils mentioned above. Despite the potential unreliability of *Seeleyosaurus guilelmiimperatoris* and *Microleidus brachypterygius*, some researchers still used them as references for flipper restoration in recent studies (e.g., [178, 158, 73]). DeBlois [179] reconstructed plesiosaur flippers based on hydrodynamic properties. But the absence of soft tissues on leading edges of flippers is not realistic, as argued by Muscutt [115], who quantitatively reconstructed plesiosaur flippers according to the wing of a penguin. No fossil discovered so far sheds light on the amount of soft tissues anterior to the leading edge of a plesiosaur flipper, thus the limbs of modern underwater fliers may be demanded as references.

2.3 Inconsistent definitions and measuring criteria

There isn't a uniform set of measuring standards in plesiosaur studies, thus measurements of the same fossil may be distinct from each other in different studies. A uniform set of definitions and measuring protocols is vital to precise estimation of body size. This demand was proposed in other areas of paleobiology (e.g., sphenacodontids [180]) but was rarely emphasized in plesiosaur studies. Therefore, a review of different measuring criteria relevant to body reconstruction is provided below.

2.3.1 Skull

Multiple terminologies and standards have been introduced as proxies for skull size of plesiosaurs. To stipulate the measuring criteria, I adopt the terminologies used by McHenry [35], who first introduced measuring methods from biomechanics to plesiosaurs. In many

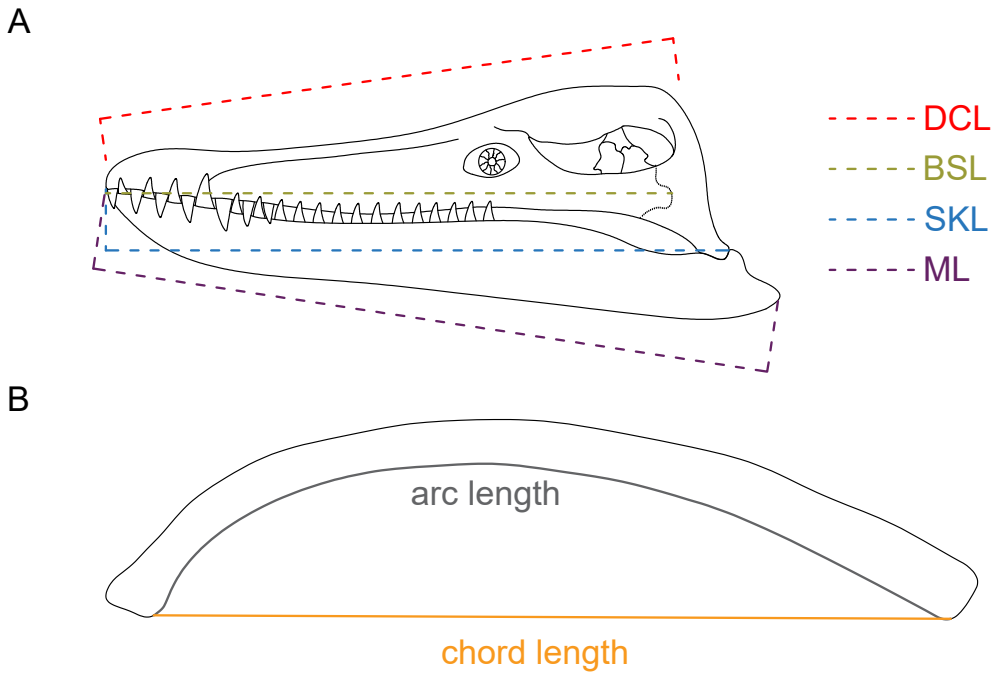

Figure 7: Illustrations showing the measuring criteria for skull and rib. **A**, different measuring methods for the skull (*Sachicasaurus vitae*). **B**, arc length and chord length of a dorsal rib. See text for detailed definitions.

cases, researchers ambiguously used the concepts "skull length" or "cranial length" without explaining their measuring standards (e.g., [181, 182, 40, 183, 53, 126, 184]). Even when clearly stated, "cranial length" or "skull length" in plesiosaurs might have various definitions in different studies. Figure 7A shows the different measuring methods for plesiosaur skull used in this paper.

Skull Length (SKL): SKL refers to anteroposterior length from tip of the snout to midline between the quadrates. It was also termed as "cranial length" in some previous studies (e.g., [185, 74]). SKL is a good proxy for skull size since other measuring criteria can be affected by taphonomy or anatomy (see below).

Basal Skull Length (BSL): BSL refers to length from tip of the snout to the basioccipital condyle [186, 187]. This criterion has a long history, dating back to the 19th century [188]. In vertebrates, the occipital condyle connects with atlas, the first cervical [45]. Therefore BSL is a good proxy for skull size since the sum of it and length of vertebral column is the total body length. BSL also has the advantage that it is less likely to be affected by taphonomic processes because the condyle lies at the same horizontal plane with the snout. However, it is not a good measuring method when comparing skull sizes of different clades of plesiosaurs. The quadrates extend far behind the basioccipital condyle in some taxa (e.g., *Rhomaleosaurus cramptoni* [189]; *Aristonectes quiriquinensis* [127]), thus BSL would have unsatisfactory performances in representing their overall skull size.

Dorsal Cranial Length (DCL): DCL refers to length along the dorsal midline of the skull. High sagittal crests are present in skulls of some plesiosaur species (e.g., [190, 191]),

thus DCL can be heavily affected by taphonomy (i.e., whether the skull is dorsalventrally crushed).

Mandibular Length (ML): There are two methods to measure the ML. The first principle is to measure from tip of the mandibular symphysis to midpoint of posterior ends of retroarticular processes [79, 113, 75]. The other principle is to measure along the ramus [192, 193, 194]. Here I avoid selecting a preferred principle, but advocate clarifying the measuring criterion in future studies.

2.3.2 Spinal segmentation

Neck: As stated above, the concept of neck is an ambiguous definition in plesiosaur studies due to inconsistent opinions on vertebral segmentation. The definition of neck length varies across studies. It may refer to length of the cervical series [38, 36, 40], length of cervical and pectoral series [50, 195] or length of cervical series and some (but not all) pectorals [35, 46]. In this paper, neck length is defined as the sum of cervical lengths and intervertebral distances anterior to them (i.e., the distance between basioccipital condyle and atlas is included, but the distance between the last cervical and the first pectoral is excluded).

Trunk: Some concepts were used as proxies for rib cage lengths of plesiosaurs, including trunk, glenoid-acetabulum length and torso. Trunk often refers to the combined length of pectorals, dorsals and sacrals in a horizontal line or along the column [34, 22]. But in some studies it means the distance between glenoid and acetabulum (e.g., [4]), identical to the definition of glenoid-acetabulum length [182]. McHenry [35] observed the positions of glenoids and acetabulums in thalassophonean pliosaurs and proposed the concept of torso. It refers to combined length of the last pectoral, all dorsals and the first two sacrals. However, the position of glenoid is not fixed in plesiosaurs due to the difference in relative scapula size. In some articulated plesiosaur fossils, anterior margin of the scapula is in the level of the first pectoral vertebra (e.g., *Albertonectes vanderveldei* [46]; *Monquirasaurus boyacensis* [74]), but this is not a uniform rule for all plesiosaurs (e.g., *Avalonnectes arturi* [22]). In this paper, the terminology trunk is used and is defined as the distance between the anterior margin of scapula to acetabulum in a horizontal line (Fig. 1A).

Tail: Tail is also a concept with inconsistent definitions in previous studies. In some cases it refers to the caudal series only (e.g., [196]), while in others it also includes sacrals posterior to the acetabulum level (e.g., [35]). The second definition is adopted in this paper (Fig. 1A).

2.3.3 Ribs

To my knowledge, the criteria for measuring plesiosaur ribs have rarely been discussed. Most previous studies provided rib lengths directly without clear definition (e.g., [37, 197, 150]). There are generally two types of measuring methods for rib length in anatomy: chord length and arc length ([198, 199]; Fig. 7B). Chord length refers to the distance between two ends of the rib, and arc length is the measurement along the inner curve or outer curve of the rib. In this paper, the arc length, defined as inner curve of the rib, is preferred because it is less likely to be affected by taphonomic processes than chord length.

2.4 Ontogeny

Plesiosaurs underwent ontogenetic shifts in anatomic features during growth. The earliest ontogenetic study on plesiosaurs was carried out on *Cryptoclidus eurymerus* [200]. Some osteological characters were selected as indicators of maturity in plesiosaurs. The most widely used criterion is the fusion of neural arches to the centra, proposed by Brown [38]. However, whether this criterion is suitable for all plesiosaurs has been questioned and challenged in recent years, because lack of vertebral fusion has been observed in some relatively large individuals from Pliosauridae, Leptoclididae and Rhomaleosauridae [193, 187, 201, 202].

Most ontogenetic studies on plesiosaurs focused on Cretaceous clades. For elasmosaurids, the concentration is the ontogenetic changes in cervical morphology and ratio. O'Keefe and Hiller [203] discovered complex ontogenetic allometry in elasmosaurids. Brum et al [204] enhanced this conclusion by revealing a morphological shift in cervicals from disc-like to can-shaped in all elasmosaur groups. For polycotylids, O'Keefe et al [205] and Byrd [206] reported allometric growth in propodials and girdle elements respectively. In pliosaurids (exemplified by *Stenorhynchosaurus munozi*), evidence of allometric growth is present in their skulls, but little is known about the ontogenetic changes of their postcranial skeletons [207].

Araújo et al [208] reported paedomorphism (i.e, histologically mature but osteologically immature) in some aristonectines, and they suggested using the terminologies "osteologically mature/immature" if an osteohistological analysis is absent. In a more recent study, Araújo and Smiths [202] discovered that paedomorphism was widespread among plesiosaur groups, especially in Rhomaleosauridae, Elasmosauridae, Pliosauridae and Polycotylidae. Given the existence of paedomorphism, results from some previous studies might be misleading. For example, UANL-FCT-R2 ("the monster of Aramberri") was estimated to be a "15 m juvenile pliosaur" [209]. Although not stated clearly, this result made an impression that there existed adult pliosaurs much larger than the 15 m juvenile in Jurassic oceans. The juvenile status of UANL-FCT-R2 was identified according to lack of fusion between neural arches and centra [209]. However, Benson et al [193] argued that sutural fusion in cervicals and dorsals might be delayed or absent in thalassophonean pliosaurs. In *Monquirasaurus boyacensis* MJACM 1, the neural arches are fused to the centra in most vertebrae except cervicals [74]. If thalassophoneans also followed a front-to-back fusion order like other plesiosaurs [83], neural arches might never become fused with cervical centra in these large pliosaurs. Another possibility is that they followed a different fusion pattern. Given these potential conditions, UANL-FCT-R2 can not be confidently identified as a juvenile, but more likely to be an adult due to its large size (see discussion for a re-evaluation of its body size).

2.5 Phylogeny and Taxonomy

Phylogeny and taxonomy also play important roles in plesiosaur body reconstructions. References to close relatives are often needed when restoring incomplete fossils, and this process requires knowledge on interspecific relationships.

The phylogeny of plesiosaurs has been revealed to be unstable [19]. In early studies Plesiosauria was divided into Pliosauroidea and Plesiosauroidea [36]. Pliosauroidea used

to contain Pliosauridae, Rhomaleosauridae and Polycotylidae, and Plesiosauroidea used to contain Plesiosauridae, Elasmosauridae and Cryptoclididae [210, 38, 211]. This taxonomic system was affected by body proportions, which have been revealed to be volatile among different clades (e.g., shortening of the neck evolved independently for multiple times [212, 213]). Benson and Drunkenmiller [20] constructed a large character matrix containing 270 morphological characters and 80 operational taxonomic units. Most contemporary phylogenies are based on revised version of this matrix, and a consensus on relationships among major plesiosaur clades has been established in recent years [23, 107]. Pliosauridae has been revealed to form a monophyletic clade with Plesiosauroidea, known as Neoplesiosauria [22]. Polycotylidae is a group within Plesiosauroidea [213]. On the other hand, there exists discrepancy in topologies inside each clade among the phylogenies from recent years, due to the incompleteness of fossil materials and the usage of incompatible matrices.

2.6 A review of plesiosaur body mass estimation

Body length and body mass are the most commonly used proxies for body size. McHenry [35] argued that body length has the advantage that it is easier to be acquired and less likely to fluctuate for an animal. Numerous studies tried to estimate body lengths of different plesiosaur taxa. A splendid example was the body length estimates for multiple elasmosaurid species provided by Welles, who offered very detailed measurements in his publications [36, 34, 214].

The body plans of plesiosaurs vary greatly across different taxa. Thus body mass may be a better proxy than length because it enables the comparison of species which are distinct in body morphotypes [35]. However, body masses of plesiosaurs remain poorly studied to date, with only a few relevant publications.

Henderson [215] reproduced three plesiosaur models according to museum mounts or published reconstructions and calculated their body volumes using mathematical slicing [9]. The three models were then used to test the stability and floating properties of plesiosaurs. Although the main theme of Henderson's study was not plesiosaur size estimation, it is the first thesis offering precisely calculated plesiosaur masses to my knowledge. However, it can not be guaranteed that old reconstructions from the 20th century are completely reliable. For example, the *Liopleurodon ferox* by Henderson was reproduced from the pliosaur model created by Newman and Tarlo [88], which possesses barely any soft tissues around its rib cage (Fig. 3F).

McHenry's [35] methods of reconstruction and establishing comparative vertebral datasets have important enlightenment and referential significance. McHenry calculated the body lengths of different pliosaurid species precisely, then estimated their body masses using a commercial model (BMNH model). However, it is unknown which fossil this model was based upon, and interspecific variations were neglected during the body mass estimations. Observations from Jurassic and Cretaceous pliosaurids suggest that body proportions were diverse within Thalassophonea [216, 217], thus the mass results provided by McHenry may not be reliable.

Paul [95] created side view images of multiple plesiosaur skeletons and provided body mass estimates for many species. The highlight of this study is that each plesiosaur taxon

possesses an independent reconstruction instead of sharing a model with proportionally similar species. However, there also exist some shortcomings. For instance, barely any soft tissues were added to the rib cages, and all dorsal ribs in each model were oriented to the same direction without gradual changes. Paul [95] stated that "approximations are often inevitable" in determining body height, but the detailed criteria were not described.

Gutarra et al [4] reproduced several plesiosaurs from orthogonal photos of museum mounts or articulated fossils, and subsequently tested their hydrodynamic performances. This is the only study to date that quantitatively restored soft tissues according to *Mauriciosaurus fernandezi*. However, museum mounts, especially those constructed more than 100 years ago, can not be fully trusted. Some old mounts have been criticized by previous researchers. For example, the *Kronosaurus/Eiectus* mount MCZ 1285 probably contains too many vertebrae, as argued by McHenry [35]; a mount of *Dolichorhynchops osborni* (FHSM VP404) was constructed with humeri and femurs reversed [218]. In addition, acquiring body widths or heights from photos of articulated fossils may be problematic as well. The rib cages in some plesiosaur fossils are collapsed (e.g., *Monquirasaurus boyacensis* [74]), thus measuring body width from photos directly would probably lead to an overestimation of body size.

In general, all previous studies estimating body masses of plesiosaurs have their shortcomings, and the results may be unreliable. The key problem is that rigorously created skeletons are lacking, hence a set of protocols for plesiosaur reconstruction is demaned to solve this issue.

3 Reconstructing missing puzzles in plesiosaur fossils

Plesiosaur fossils are often incomplete or fragmented, lacking key structures for body reconstruction. Therefore some methods and criteria are required to restore the missing parts. There are two types of methods to restore the missing structures of plesiosaur skeletons: comparison and regression. The principles and applying scopes of these two methods are different.

The principle of comparison is to restore the missing parts using body ratios of close relatives. The body plans of plesiosaurs vary greatly across clades, but congeneric species normally have similar proportions and vertebral numbers (e.g., *Rhomaleosaurus* spp. [76]; *Hauffiosaurus* spp. [53]; *Styxosaurus* spp. [219, 34]; but see the significant difference in cervical number between *Microcleidus melusinae* and other *Microcleidus* species [79, 183, 220]). Thus during the process of comparison, phylogeny and taxonomy should be taken into consideration. Comparison has been frequently used in plesiosaur size estimations (e.g., [221, 222, 149, 223]). However, subjectivity can never be ruled out from this method because one can freely change the referred individual, and normally this leads to different results.

Regression is to dig the correlations between different skeletal elements in plesiosaurs using well preserved fossil materials. Previous researchers have developed some regression equations for reconstructing skeletal elements of plesiosaurs. These equations are reviewed and commented in this paper (see below). Some new relationships are also discovered and presented (Fig. 8). A common question when using regression methods is that whether the studied species follow these relationships [16]. For instance, a regression based solely

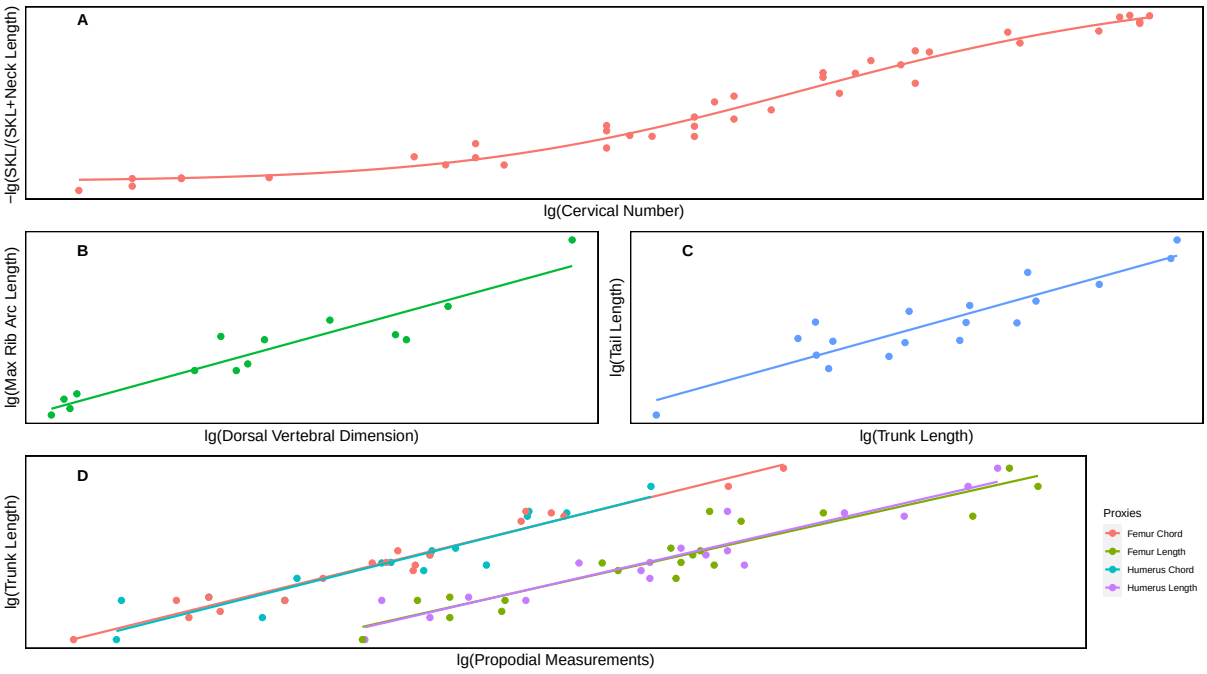

Figure 8: Regressions for reconstructing missing body parts of plesiosaurs. All measurements are in mm. **A**, Neck-SKL regression. **B**, Dorsal Vertebrae-Rib regression. **C**, Trunk-Tail regression. **D**, Propodial-Trunk regressions.

on large pliosaurs may not have good performances in predicting the values of elasmosaurs due to their great difference in body proportions. To ensure that the equations can be applied to the whole Plesiosauria, all regressions in this study were summarized from datasets which are phylogeneticly widespread, unless available samples are extremely rare.

3.1 Skull size

Knutsen et al [187] established two regression equations to estimate the BSL of pliosauroids based on cervical width and condylar width respectively. These are the only regression equations applied for skull size in plesiosaurs to date. However, there exist some problems in the datasets from current perspective. In condylar width-BSL regression, half of the specimens are from Rhomaleosauridae, a clade revealed to be relatively distinct from Pliosauridae in recent plesiosaur phylogenies (e.g., [19, 23]). In cervical width-BSL regression, three out of eight samples included in the dataset are juveniles. The growth pattern of pliosaur vertebrae has not been studied, but it is possible that cervical ratios of juveniles are different from those of adults, as in elasmosaurids [203, 204]. In cervical width-BSL regression, the juveniles gather at lower ends of the axes due to their small sizes, and this may lead to biased estimates.

The width of basioccipital condyle serves as a proxy for anterior cervical width, so the two regression equations both try to reveal the relationship between skull size and cervical width (Espen Knutsen, pers. comm, 2022). However, it is uncertain whether cervical width is a good proxy for skull size in plesiosaurs. There exist some conspecific plesiosaurs in which the ratio of skull size to cervical width varies greatly (e.g., *Muraenosaurus leedsi*, see [41]).

There is an empirical consensus that long-necked plesiosaurs possess small skulls and short-necked forms possess large skulls [25]. Inspired by this empirical conclusion, I established a new regression equation based on SKL, neck length and cervical number. SKL was selected because it is a better proxy than BSL when comparing skull size, as stated above. To enlarge the dataset, individuals with a complete but disarticulated cervical series were included, with their intercervical distances restored according to close relatives. The two variables in this regression are:

$$x = \log_{10}(\text{Cervical Number}) \qquad y = -\log_{10}\left(\frac{\text{SKL}}{\text{SKL} + \text{Neck Length}}\right)$$

I used a log-logistic function to perform a nonlinear regression [224], which corroborates the conjecture that there is a negative correlation between skull size and neck length in plesiosaurs (Fig. 8A). The math equation behind this correlation is:

$$y = \frac{-1.1729}{1 + \left(\frac{x}{1.5739}\right)^{11.9871}} + 1.3651 \tag{1}$$

The dataset is phylogeneticly widespread and contains 40 species, ranging from *Monquirasaurus boyacensis* (11 cervicals [74]) to *Albertonectes vanderveldei* (75 cervicals [46]). Therefore this equation can be applied to the whole Plesiosauria.

3.2 Rib length

Ribs are key structures for rib cage reconstructions. However, rib length information is often lacking because many plesiosaur fossils contain incomplete or distorted ribs. In addition, the mounted status of some plesiosaur skeletons also precludes measurements. For this reason, I developed a regression method to estimate maximum rib length using measurements of dorsal vertebrae. The two variables in this regression are:

$$x = \log_{10}(\text{Average Dorsal Length} \times \text{Average Dorsal Width} \times \text{Average Dorsal Height})$$

$$y = \log_{10}(\text{Maximum Rib Arc Length})$$

and the equation behind their relationship is

$$y = 0.3520x + 0.7177 \qquad (r^2 = 0.8853,\ p < 0.001) \tag{2}$$

Only plesiosaur individuals with relatively complete dorsal rib series were included as samples to ensure that all data were measured from the longest rib of each individual. The requirement for completeness of the fossil restricted the dataset to 15 species, with rhomaleosaurids and leptoclidids absent due to the lack of their vertebral measurements. The regression shows that there is a positive correlation between combined dorsal vertebral dimensions and maximum rib length (Fig. 8B).

3.3 Tail length

No regression equation has been established to estimate tail length to my knowledge. I gathered samples from different plesiosaur clades and established a regression to estimate tail length using trunk length (Fig. 8C):

$$y = 0.7912x + 0.6513 \qquad (r^2 = 0.8217,\ p < 0.001) \tag{3}$$

where

$$x = \log_{10}(\text{Trunk Length}) \qquad y = \log_{10}(\text{Tail Length})$$

The dataset contains only 15 samples due to the generally poor preservation of plesiosaur tails. In addition, polycotylids are not included in this regression since regression diagnostics revealed that they are outliers and would cause significant impact. Although it is consistent with the conjecture above that short tail is a synapomorphy of polycotylids, this result was summarized from limited amount of samples (*Dolichorhynchops* and *Mauriciosaurus*) and might be biased by poor fossil sampling. It is possible that other polycotylids possessed longer tails, but more complete fossils are required to illuminate this issue. Before that, I recommend not to predict tail lengths of polycotylids using this equation.

3.4 Trunk length

O'Gorman et al [149] revealed the correlation between femur length and dorsal region length in elasmosaurids based on eight species. This regression was restricted to elasmosaurids. To develop equations that can be applied to the whole Plesiosauria, I collected trunk length and propodial measurements from literature. Trunk length, instead of dorsal region length, was selected because it enables the inclusion of fossils which show their ventral sides. It is also a better proxy for body size than dorsal region length due to the variation of pectoral and sacral numbers in plesiosaurs. Four variables (humerus length, humerus chord, femur length and femur chord) were tested, and the results are:

$$\log_{10}(\text{Trunk}) = 0.9954 \log(\text{Humerus Length}) + 0.5776 \qquad \left(r^2 = 0.8985,\ p < 0.001\right) \quad (4)$$

$$\log_{10}(\text{Trunk}) = 1.0877 \log(\text{Humerus Chord}) + 0.6964 \qquad \left(r^2 = 0.8757,\ p < 0.001\right) \quad (5)$$

$$\log_{10}(\text{Trunk}) = 0.9676 \log(\text{Femur Length}) + 0.6424 \qquad \left(r^2 = 0.8782,\ p < 0.001\right) \quad (6)$$

$$\log_{10}(\text{Trunk}) = 1.0647 \log(\text{Femur Chord}) + 0.7515 \qquad \left(r^2 = 0.9629,\ p < 0.001\right) \quad (7)$$

Only articulated fossils with measurable trunks were included, and the dataset contains 20 samples which are phylogeneticly widespread. Regression results suggest that propodial measurements are good indicators of trunk length (Fig. 8D), and the best proxy is femur chord with r^2 over 0.96.

3.5 Limb length

Sanders [117] established several regression equations to estimate limb lengths of plesiosaurs from chord propodial, chord epipodial and chord digits respectively. The dataset behind these equations contains 45 plesiosaur species from a wide phylogenetic range, thus they can be applied to the whole Plesiosauria. Since the prododial chords can be obtained easily, the equation based on it is adopted in this paper:

$$\ln(\text{Chord Propodial}) = 0.9952 \ln(\text{Flipper Length}) - 1.6985 \qquad (r^2 = 0.8937) \quad (8)$$

4 Criteria for plesiosaur reconstruction

4.1 Body length calculation

The first step to reconstruct a plesiosaur is to calculate its body length. Body length along the vertebral column consists of basal skull length (BSL), sum of vertebral lengths, sum of intervertebral distances and thickness of soft tissues.

4.1.1 Length of vertebral column

The criteria for calculating spinal length are described first since estimating skull size requires neck length and cervical number. If the plesiosaur fossil is articulated or broken into several blocks, its spinal length can be acquired by summing the measurements along the column. But the fragmented and disarticulated nature of many plesiosaur fossils suggests that a set of methodology is needed for estimating their spinal lengths. When dealing with relatively complete vertebral columns, of which only a few vertebrae are missing or unmeasurable, lengths of those vertebrae can be restored by taking the average values of adjacent ones. If many vertebrae are missing or badly preserved, a close relative with a complete vertebral column is selected for reference. McHenry [35] emphasized the importance of comparative datasets of vertebral lengths in plesiosaur reconstructions. Order of vertebrae in the studied individual should correspond to that of the referential individual. The assumption behind this criterion is that closely related species have similar vertebral length distributions. For example, if the longest dorsal vertebrae are positioned in middle of the trunk in one species, it is possible that its close relatives also follow this pattern.

The intervertebral distances can be measured directly if the fossil is articulated. But these cartilages are often not present in disarticulated columns. Instead of assuming absolute values, I advocate estimating intervertebral distances with ratios from closely related species which have articulated columns, following Troelsen [54]. As stated in the preliminaries, the ratio of intervertebral distances to vertebral lengths in the pectoral, dorsal and sacral regions seems to be uniformly around 10% in different plesiosaur clades, hence only the estimation of intercervical distances requires comparison with relatives.

Before estimating the tail lengths of incomplete individuals, their trunk lengths need to be acquired. Trunk length can be measured directly if the fossil contains gridles *in situ*. If this condition can not be satisfied, a comparison method should be applied: the ratio of length along the vertebral column to length in a horizontal line of the trunk region in a referential model can be used to estimate the trunk length of the studied species. Afterwards the tail length can be predicted using Trunk-Tail regression (Eq. 3) or comparison method.

4.1.2 Skull length

Basal skull length (BSL) in plesiosaurs is not always available. In some plesiosaur fossils exposed in dorsal view, their basioccipital condyles may be obscured by the overlying skull rooves, thus the BSLs are unmeasurable. Comparison with relative species is required in such cases to convert their SKLs to BSLs. The skulls of some fossils are fragmented or even missing. The Neck-SKL regression (Eq. 1) is used to predict the SKLs of these individuals if their neck lengths can be measured or estimated. Comparison with congeneric species which possess neck and skull measurements is also applied to provide other possible results. Then average value of the results is taken as the estimated SKL, which is finally converted to BSL by comparison.

4.2 Rib cage reconstruction

Trunk length of the studied plesiosaur is measured or estimated in body length calculation stage, then curvature of the spine can be reconstructed by setting the scapulae at the level of the first pectoral and acetabulum between the first two sacrals. To enable the calculation of body volume and surface area, three thoracic cross-sections are reconstructed for each individual: the glenoid cross-section (the vertical plane containing the glenoid; Fig. 9B), the acetabulum cross-section (the vertical plane containing acetabulum; Fig. 9D) and the maximum cross-section (which is set to be at the middle of the other two cross-sections; Fig. 9C). Each cross-section is split into the dorsal part and ventral part. All the dorsal parts of the three cross-sections include vertebrae and ribs. In the glenoid and acetabulum cross-sections, the ventral part consists of the coracoids and pubes respectively, and the ventral part of maximum cross-section is gastralia. The size and shape of each cross-section are determined in this stage.

4.2.1 Glenoid cross-section

The two coracoids formed a V-shape in life [41], but the angle between them can not always be confidently inferred from fossils. A mathematical method is applied here to determine the width and height of the glenoid cross-section. In some previous reconstructions or mounted plesiosaurs (e.g., *Thalassomedon haningtoni* DMNH 1588 and *Hydrotherosaurus alexandrae* UCMP 33912 [36]), the dorsal part and ventral part at the glenoid level are of the same width. This assumption is inherited in this paper to reconstruct the glenoid cross-section. The first step is to obtain lengths of the ribs in the glenoid plane. Arc lengths of these ribs can be calculated using the rib length distribution (i.e., the ratio of arc length in glenoid cross-section to that of the longest rib) of closely related species which have complete rib series. Lengths of transverse processes in glenoid cross-section can be acquired in a similar manner if they are not preserved. The ribs are firstly placed with angle α and β both set to 0 degree (Fig. 9B), for which the reason is clarified in the preliminaries. This determines width of the glenoid cross-section and height of the dorsal part. With width of coracoid at hinder angle of glenoid, height of the ventral part can be calculated by the Pythagorean theorem.

4.2.2 Acetabulum cross-section

The pubes and ischia of plesiosaurs also formed V-shapes in life [41]. However, width and height of the acetabulum cross-section can not be calculated using the same method applied in the glenoid region. This is because the dorsal ribs of plesiosaurs shrink in size and tend to become stragit in posterior half of the dorsal region (see preliminary section). In this paper, it is assumed that width of the acetabulum cross-section is the same with that of the glenoid cross-section. This assumption is corroborated by the *in situ* fossil of *Maurciosaurus fernandezi* [47]. The lower end of the ventral part is set to be in the same horizontal line with the glenoid. Using these criteria, width and height of the acetabulum cross-section can be calculated (Fig. 9D).

4.2.3 Maximum cross-section

Dorsal part of the maximum cross-section can not be reconstructed with vertebrae and a single pair of ribs because of the presence of slant angles. The method applied by Welles to reconstruct *Hydrotherosaurus alexandrae* [36], which requires multiple pairs of dorsal

ribs to obtain the cross-sectional profile, is adopted here. Arc length of the longest rib is first estimated using regression (Eq. 2) if it is unavailable, and it is assumed that several ribs in middle of the trunk are similar in length. Dorsal ribs are initially placed without inclination, then heights and widths of them are multiplied by $\cos\alpha$ and $\cos\beta$ repestively. The maximum cross-section can be regared as part of a vertical plane that truncates the rib cage, and the positions of dorsal ribs intersecting with the plane are determined. Finally a smooth curve is used to link all the intersection points (Fig. 9C). Height of the ventral part can be acquired with the following approach: average height of the ventral parts of glenoid cross-section and acetabulum cross-section is taken, then the result is scaled by multiplying the inverse of rib length distributional proportion which is used in estimating rib lengths in glenoid level.

4.3 Flipper elements

Plesiosaur flippers can be completely preserved only in rare cases (e.g., [225, 219]), thus restoration is frequently required. If propodial of the studied flipper is preserved, total length of the whole limb is first estimated using regression (Eq. 8) or comparison. Then missing elements are restored according to the shapes and ratios of corresponding ones in close relatives. If a pair of forelimbs or hindlimbs are entirely missing, flipper lengths are restored using comparison with congeneric or kin species.

4.4 Soft tissue reconstruction

4.4.1 Skull and neck

The soft tissues added to the skull region are very thin, as suggested by the anatomy of leatherback turtle (*Dermochelys coriacea*) [133], but enough soft tissues beneath the skull are reconstructed to create a smooth curve connecting skull and neck so that there doesn't exist an abruptly humped chest. No soft tissues are reconstructed anterior to the head to increase body length. This is unrealistic due to the presence of skin, but its thickness is negligible comparing to the whole body and would not cause significant impact on overall body size.

4.4.2 Rib cage

Soft tissues around the rib cage are reconstructed according to *Maurciosaurus fernandezi*, and the detailed criteria are described below. The rib cage of *M. fernandezi* is collapsed ([47]: Fig. 8), thus the soft tissues were proportionally thicker in life than the fossilized condition. For this reason, the rib cage of *M. fernandezi* was first reconstructed according to the criteria described above. Muscles, fat and skin can not be differentiated from the imprints around the fossil, hence soft tissues are only restored numerically. The fossil of *M. fernandezi* demonstrates that plesiosaurs possessed thicker musles for locomotion in the girdle regions than in middle of their trunks. The soft tissue outlines of the glenoid and acetabulum cross-sections are 45% thicker than the rib cage, and this proportion decreases to 30% in middle of the trunk. The fossil of *M. fernandezi* provides no evidence for the amount of dorsalventral soft tissues, but in modern marine mammals the cross-sectional outlines share the same shape with corresponding cores (Fig. 5CDE). Hence a smooth curve is first drawn along the rib cage, leaving enough space for musles around neural arches and giving the studied plesiosaur a rounded cross-section. Outline of the acetabulum

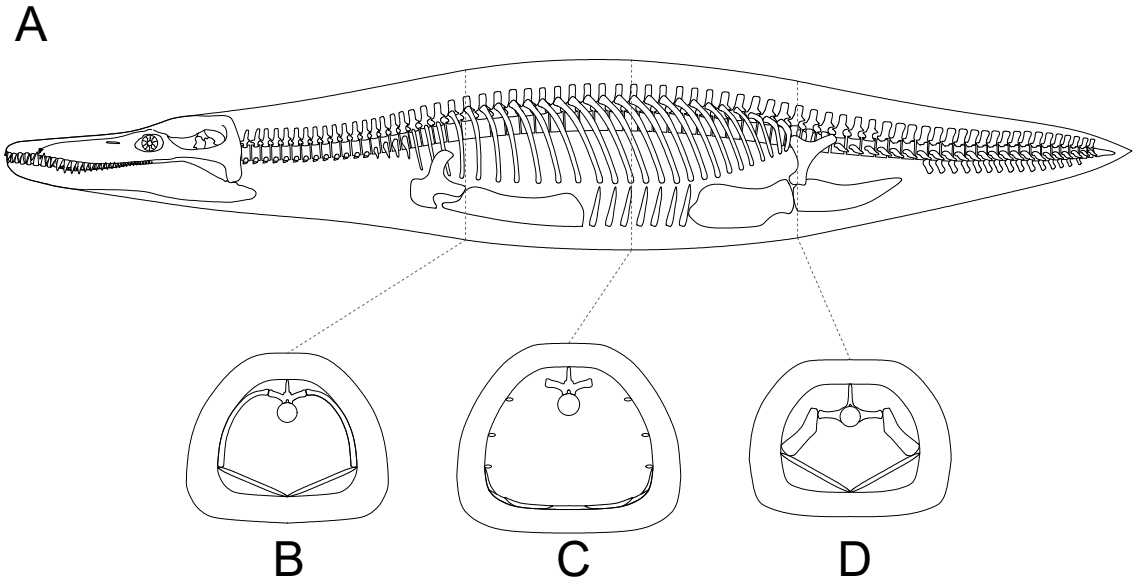

Figure 9: Reconstruction of *Pliosaurus* cf. *kevani* (CAMSM J. 35990) under the criteria proposed in this study. **A**, main body of the model, with limbs removed. **B**, glenoid cross-section. **C**, maximum cross-section. **D**, acetabulum cross-section.

cross-section is constructed by scaling and stretching that of the glenoid cross-section. Then the soft body profiles are obtained by magnifying the cores. Figure 9 shows the *Pliosaurus* model reconstructed under the criteria proposed above (see supplementary materials for detailed methods).

4.4.3 Tail and flippers

The fossil of *M. fernandezi* shows a compressed tail, and trunk outline continues to it [47]. It is assumed here that there wasn't abrupt undulation of the body outline between trunks and tails in other plesiosaurs either. Lower and upper ends of the acetabulum cross-section are linked to tip of the tail (5% extra length representing soft tissues added according to *Seeleyosaurus guilelmiimperatoris* [119]) with smooth curves. Tail fins of plesiosaurs are provisionally not reconstructed since their shapes and orientations are not certain in the current stage, and neglecting the tail fin would not make a significant impact on total mass and area. No fossil evidence so far sheds light on complete outlines of plesiosaur flippers in life, hence I follow the method proposed by Muscutt [115] to reconstruct flipper profiles according to penguins (see [115] for details).

4.5 Body density

The last step is assigning density to transform volume into mass. Animals are not solid objects but possess cavities including lungs and digestive tracts, which should be taken into consideration during mass estimation [226, 11, 16]. However, this task is tricky in studying extinct animals since direct evidence is often lacking. Anatomy of modern animals may shed some light on this issue, but it is not always certain that two different clades share the same pattern. Henderson [215] assigned lungs occupying 10% the total body volume for plesiosaurs, which is the upper end of relative lung size range in extant reptiles. Richards

[90] proposed lungs occupying 9.8% of total body volume for the same reason. However, it is not certain that whether plesiosaurs followed the typical reptile pattern. Another tricky problem is that lung size varies across species within a clade. Deep-diving whales are known to possess smaller lungs than their shallow-diving relatives [227]. It is likely that lung size also varies among different plesiosaurs. In addition, lung sizes do not remain the same in modern marine mammals since they collapse during diving [228, 229, 230]. Sea turtles also possess collapsible lungs [231, 232, 233]. Currently the diving mechanism of plesiosaurs are unclear, so I avoid designating lung sizes but assume that they were neurally buoyant (overall body density set to 1025 kg/m^3).

5 Methods

5.1 Model construction

I made 22 plesiosaur models under the criteria proposed above (reconstruction details can be found in supplementary materials). All models are two dimensional and are in lateral view, with three cross-sections (glenoid, maximum and acetabulum) and limbs. Each model is representative of a genus (except *Pliosaurus* cf. *kevani* and *P. funkei*, see below for reason) since intrageneric differences in body plans can not be quatatively studied in the current stage. The models are phylogeneticly widespread, consisting of genera from all major plesiosaur clades. All models were made in AutoCAD 2020, which has high precision and has been applied in reconstructing extinct animals in previous studies [9, 215]. The accuracy of each model was set to four digits after the decimal point during construction. Skeletal measurements were cited from literature or acquired from high-resolution photos provided by colleagues.

5.2 Body volume and surface area calculation

After the models were constructed, I used the cross-sectional method (CSM) to calculate their volumes and surface areas [234]. CSM processes cross-sectional profiles directly instead of assuming an elliptical or superelliptical approximation. It integrates areas (or circumferences) of the cross-sections to mass (or surface area). I assume that body cross-sections of plesiosaurs shifted gradually in life, which is also the principle behind CSM. Each model was partitioned into 4 parts ("slabs" in cross-sectional method [234]) by the three cross-sections. Identidy segments, which are maximum heights of the three cross-sections in this case, were drawn and measured. Then area and circumference of each cross-section were obtained using *measuregeom* command in AutoCAD. Parameters φ and ψ required in cross-sectional method were calculated afterwards. The slabs at two ends of the sagital axis were treated as cones with constant φ and ψ values. The other two in the trunk region were treated as frustums with gradually changing cross-sections. Each slab was sliced into 1000 subslabs using *arrayrect* and *trim* in AutoCAD, and *dataextraction* was applied to export the identity segments into Excel, where the final calculation took place. Volumes and lateral areas of the four slabs were added together to acquire the total volume and surface area of the main body respectively. All limbs were treated as cones with costant φ and ψ values. Assumed cross-section of limbs was reproduced from Muscutt [115]. Their volumes and areas were calculated in the same way with the main body.

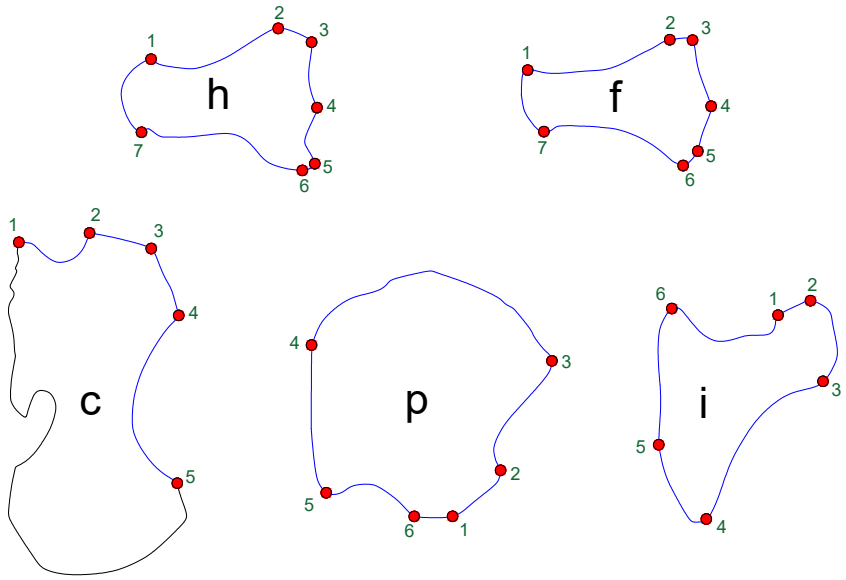

Figure 10: Landmarking schemes of the selected bones. Red points represent landmarks. Semilandmark curves are marked in blue. Abbreviations: h, humerus; f, femur; c, coracoid; p, pubis; i, ischium.

5.3 Morphometric analysis

To clarify whether there exist correlations between sizes of skeletal elements and body volume, centroid sizes of some bones were obtained and tested. I collected images of humeri, femurs, coracoids, pubes and ischia of the 22 model individuals from literature. Scapulae were not included due to their complex three-dimensional structures, and they are not preserved in some model individuals. If a skeletal element is not preserved or incomplete, it was not included in the dataset. All images were scaled to correct size in tps.dig2 using centimeters before landmarking. I used landmarks and semilandmarks to quantify the geometry of the skeletal elements. Placement schemes of the constellations are shown in figure 10, and the detailed explanation behind each landmark can be found in supplementary materials. After the landmark files were constructed, they were imported into R 4.1.3 [235] using geomorph package [236, 237]. A Procrustes analysis was performed, then centroid sizes were extracted for analyses.

Besides centroid sizes, some linear measurements were also collected, including lengths and widths of the skeletal elements mentioned above. Measuring criteria of each element can be found in supplementary materials. Trunk lengths and dorsal dimensions (defined as average dorsal vertebral length $\times$ average dorsal vertebral width $\times$ dorsal vertebral height) data were also gathered.

5.4 Regressions

I used linear regressions to generate equations for predicting the sizes of missing body parts in plesiosaurs, except for Neck-SKL equation. Regression diagnostics were performed to winnow and eliminate outliers. I avoided using confidence intervals or prediction intervals since plesiosaur reconstructions allow only point estimations to enable volume and area calculation. For Neck-SKL equation, a nonlinear least sqaure method was used, and I

Table 2: Volumes and areas of the models

Model	Catalogue Number	Body Length	Volume	Surface area
Abyssosaurus	MChEIO PM/1	6767 mm	1.3862 m^3	12.7017 m^2
Albertonectes	TMP 2007.011.0001	12134 mm	4.3496 m^3	26.0802 m^2
Aristonectes	SGO.PV.957	10000 mm	5.7628 m^3	32.5928 m^2
Cryptoclidus	NHMUK PV R2860	3739 mm	0.4280 m^3	5.4443 m^2
Dolichorhynchops	FHSM VP404	2958 mm	0.5250 m^3	5.3066 m^2
Hydrotherosaurus	UCMP 33912	8835 mm	2.2297 m^3	18.6510 m^2
Kronosaurus/Eiectus	MCZ 1285	10390 mm	13.0233 m^3	46.2238 m^2
Liopleurodon	GPIT-RE-3184	5854 mm	2.9214 m^3	17.3344 m^2
Macroplata	NHMUK PV R5488	4627 mm	0.8940 m^3	8.0467 m^2
Martinectes	KUVP 40002	4585 mm	1.4144 m^3	11.7607 m^2
Mauriciosaurus	INAH CPC RFG 2544 P.F.1.	2007 mm	0.0829 m^3	1.6625 m^2
Monquirasaurus	MJACM 1	9108 mm	13.6487 m^3	43.6918 m^2
Peloneustes	GPIT-RE-3182	4337 mm	1.4363 m^3	10.7135 m^2
Pliosaurus cf. *kevani*	CAMSM J. 35990	9776 mm	12.5749 m^3	42.5029 m^2
Pliosaurus funkei	PMO 214.135	9776 mm	12.7247 m^3	46.7229 m^2
Polycotylus	YPM 1125	4676 mm	1.1222 m^3	9.5767 m^2
Rhomaleosaurus	NHMUK PV R4853	6820 mm	3.4062 m^3	21.6122 m^2
Sachicasaurus	MP111209-1	10233 mm	16.7108 m^3	53.2342 m^2
Stenorhynchosaurus	VL17052004-1	5979 mm	2.7952 m^3	16.9390 m^2
Styxosaurus	SDSM 451	11283 mm	4.0494 m^3	26.9084 m^2
Thalassomedon	DMNH 1588	11978 mm	7.2257 m^3	34.8474 m^2
Vegasaurus	MLP 93-I-5-1	6186 mm	1.2219 m^3	11.0328 m^2

selected a four-parameter log-logistic function to perform fitting [224], which is in the form of

$$y = \frac{A_1 - A_2}{1 + \left(\frac{x}{\theta}\right)^{\lambda}} + A_2$$

All data were collected from published literature, and the datasets were uploaded as supplementary materials.

Linear regression was also applied to test which skeletal element is a good indicator of body size and to generate scaling equations for quick body size estimation. I used body volume rather than mass in order to leave room for altering body density if future discoveries shed light on this issue. I used r^2 and p-values to evaluate the regression models.

All data were imported into R 4.1.3 [235] and $\log_{10}$ transformed before analyses. Linear regressions were performed using lm( ) function. Non-linear regression was performed using drm( ) from drc package [238]. Function type was set to LL.4( ), which activates a self-starting four-parameter log-logistic curve fitting. Results of regressions were plotted using ggplot2 [239], ggpubr [240] and cowplot packcage [241].

6 Results

Body volumes and surface areas of the 22 plesiosaur models are listed in Table 2. Figure 11 shows the results of linear regressions tesing correlations between skeletal elements and body volume. Coefficients, r^2 values and p-values of them are shown in Table 3.

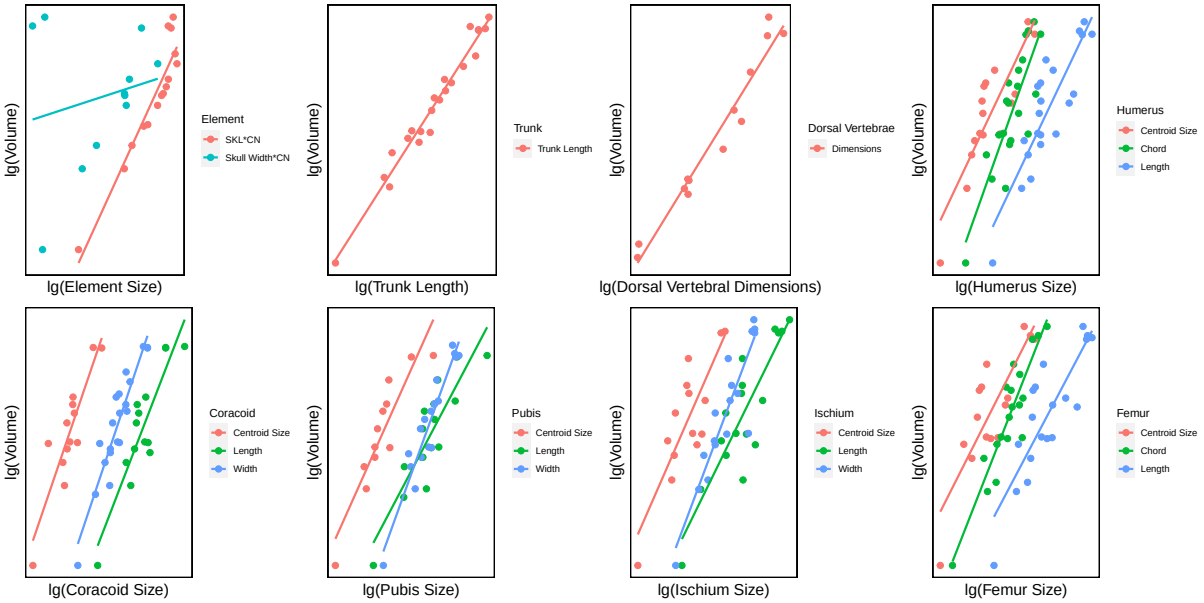

Figure 11: Linear regressions showing correlations between skeletal sizes and body volume. CN is short for cervical number. Skull width represents maximum width of skull across quadrates.

p-value smaller than 0.001 is considered significant in this study. Regression results suggest that skull width multiplied by cervical number is not significantly related to body size, other selected elements all show positive correlations with volume. Therefore, sizes of these skeletal elements can be regarded as indicators for plesiosaur body size. The best two proxies are trunk length and dorsal vertebral dimensions (defined as avergae length×average width×average width), with r^2 values larger than 0.95. These scaling equations offer tools for quick body size estimation and can generate predictions from very fragemented materials. Centroid sizes of some skeletal elements were tested because they evaluate the overall size better than linear measurements, but it turns out that they don't always have better performances in predicting body size.

7 Discussion

7.1 On some large Jurassic pliosaurs

Since the erection of genus *Pliosaurus* [242], much attention, from either paleontologists or the public [243], has been paid to the body sizes of thalassophonean pliosaurs. They were one of the first groups of giants discovered, and accompained the development of modern paleontology [35]. With the burst of plesiosaur research during the past two decades, the body sizes of large Cretaceous pliosaurs gradually come to light: from *Monquirasaurus boyacensis* (14 t [74]), to *Kronosaurus/Eiectus* (QM F2454 weighed 15.5 t [35]), to *Sachicasaurus vitae* (17 t [39]). However, body sizes of some large Jurassic pliosaurs remain mysterious due to the fragmented nature of their fossils. A review of these materials was carried out by McHenry [244, 35], but here I present a comprehensive review again since the methods and criteria used by McHenry were quite different from those proposed in this paper.

Table 3: Coefficients of volume scaling equations. Trunk lengths before $\log_{10}$ transformation are measured in m, other linear measurements are in mm. Unit for body volume is m^3. n represents sample number and CN is short for cervical number.

Element		n	Slope	Intercept	r^2	p-value
Skull	skull length×CN	15	2.1643	-8.8515	0.8847	<0.001
	skull width×CN	11	0.3218	-0.7794	0.0419	0.5461
Trunk	trunk length	22	2.7938	-0.4095	0.9701	<0.001
Dorsal Vertebrae	dimensions	13	0.9959	-5.4570	0.9561	<0.001
Humerus	centroid size	17	2.6135	-5.4451	0.7817	<0.001
	length	21	2.6053	-6.5481	0.7569	<0.001
	chord	21	3.4785	-7.9156	0.7091	<0.001
Coracoid	centroid size	13	2.8724	-5.5306	0.7995	<0.001
	length	14	2.5376	-6.7231	0.8065	<0.001
	width	20	2.9160	-6.9805	0.8724	<0.001
Pubis	centroid size	12	2.7708	-5.8606	0.8397	<0.001
	length	15	2.3471	-5.8830	0.7760	<0.001
	width	17	3.4380	-8.6042	0.9062	<0.001
Ischium	centroid size	14	2.5175	-5.1651	0.7069	<0.001
	length	17	2.2407	-5.5707	0.7669	<0.001
	width	17	2.9425	-6.9815	0.8311	<0.001
Femur	centroid size	15	2.4302	-5.0194	0.7089	<0.001
	length	19	2.3287	-5.8636	0.7248	<0.001
	chord	19	3.1413	-7.1047	0.8430	<0.001

It should be noted that estimating body size from fragmented fossils may be complicated, and the results can be problematic. Some previous studies compared incomplete fossils with different referential species and provided intervals to bracket the true sizes (e.g., [35, 223]). However, some results produced this way may not be reliable given the flexible body plans of plesiosaurs during their evolutionary history [25], thus restricting referential models to congeneric species or coeval relatives may be a better option. For example, the reconstructions of Jurassic pliosaurs are sometimes affected by species from Brachaucheninae, a monophyletic Cretaceous clade consisting of pliosaurs with extremly short necks [20, 245] (except for *Stenorhynchosaurus munozi* [246]; *Lorrainosaurus keileni* from Bajocian was also revealed to be a brachauchenine recently, but this result is questionable due to the incompleteness of its holotype [247]). There is, however, no evidence that extremely short necks have been evolved in Jurassic thalassophoneans, and observations from *Liopleurodon*, *Peloneustes* and *Pliosaurus* fossils suggest that their necks are comparative to or just slightly shorter than SKLs [111, 43, 248].

Before the review, the referential models used for comparison merit an introduction. Fragmented materials were compared with either *Liopleurodon* model or *Pliosaurus* model established in this study to estimate their body sizes, depending on their stratigraphic horizons. The *Liopleurodon* model was based on GPIT/RE/3184, an old mount that was described by Linder [111]. The vertebral count in the current mount exceed the number

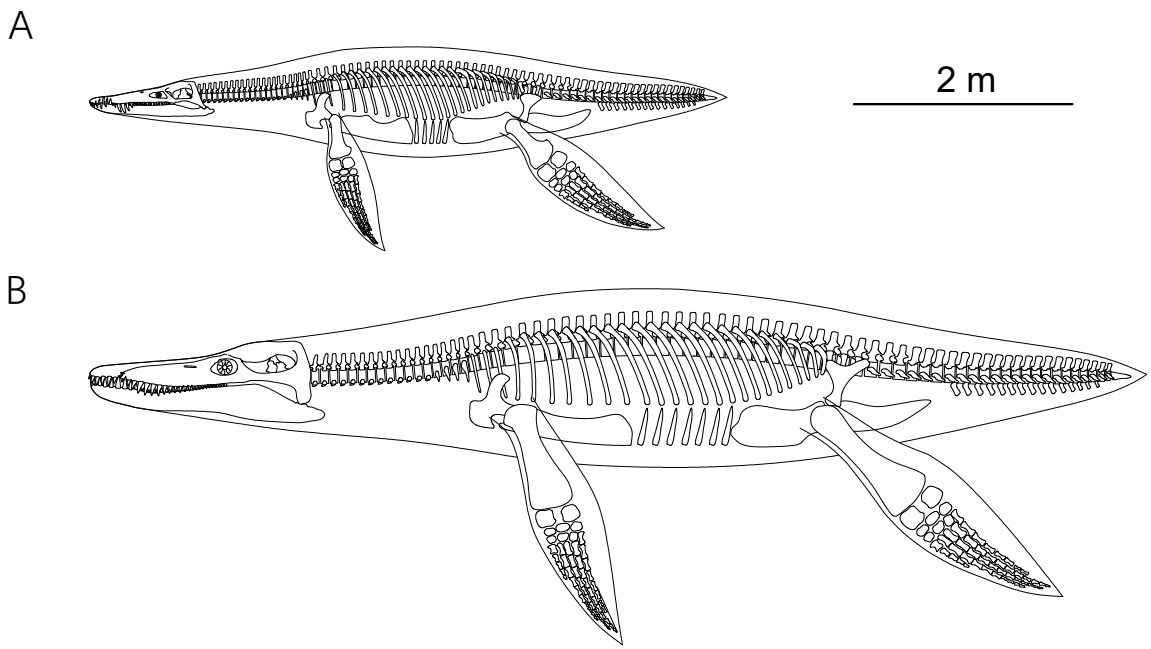

Figure 12: Body reconstructions of *Liopleurodon ferox* and *Pliosaurus funkei*. **A**, *L. ferox* GPIT/RE/3184. **B**, *P. funkei* PMO 214.135. Limbs are set in a vertical plane for display. The skull of *P. funkei* is reproduced from that of *P. kevani* since it is not preserved. Its morphology may not be reliable, but this would not cause significant influence on body size estimation.

recorded by Linder (pers. obs; Fig. 3C) and approaches the vertebral formula of NHMUK PV R3536 [43]. The caudal series is incompletely preserved (only 13 caudals were reported by Linder), and tail of the mount was restored, being too short if *Liopleurodon* had a trunk-tail proportion similar to that of *Peloneustes* [43]. Hence the tail length in the model was restored using Trunk-Tail regression (Eq. 3), and the spinal curvature was rearranged (Fig. 12A).

The *Pliosaurus* model is a mixed model, based on *P.* cf. *kevani* CAMSM J. 35990 and *P. funkei* PMO 214.135 [110, 187]. As stated above, cervical width may not be a good proxy for skull size, and vertebral lengths in corresponding regions indicate that these two individuals were comparative in body size. This is further supported by their similarity in coracoid size ([110]: Fig. 4; [187]: Fig. 9). From this perspective, the other individual of *P. funkei*, PMO 214.136, was also similar in size to the model. In addition, estimated SKL of the model is almost identical to that of *P. kevani* DORCM G. 13675 [193]. Therefore, all these four individuals were around 9.8 m and weighed over 12 t (Fig. 12B), behind which the core assumption is that different *Pliosaurus* species possessed very similar body plans.

Large pliosaurs that might reach or exceed 10 m in length first appeared in Callovian. Gilbert [249] mentioned a giant individual from Oxford Clay Formation that posesses "a right-hand paddle 7 feet 6 inches in length". Newman and Tarlo [88] also reported briefly that the "distance across the paddles is 21 feet" and estimated a 36 feet (nearly 11 m) body length for this individual. Comparison of its hindlimb with that of *Liopleurodon ferox*

suggests a 9.4 m body length. But I would agree with McHenry [35] that it might fall within the range of 9∼11 m if taking limbspan into consideration. This individual, known as "the Stewartby pliosaur", is currently housed in NHMUK, with catalogue number R8322. A more detailed body size estimation is not applicable in the current stage, pending the reassessment of this fossil. Its existence demonstrates that giant pliosaurs already occurred in Callovian oceans. Another fossil, which is a large mandible fragment known as the "NHM symphysis" in [35], further corroborates this conclusion. McHenry [35] mentioned an isolated vertebra from Peterborough (PETMG R272). Size of its owner was once thought as 15∼18 m, and later decreased to 11.6∼14.2 m. Although McHenry mentioned the possibility that it is in fact from a sauropod, its dinosaur identity was not agreed by everyone at that time. It is worth mentioning that this fossil has been restudied recently and revealed to be a sauropod indeed [250].

Megalneusaurus rex from Oxfordian of Wyoming was regarded as a very large pliosaur [35]. The incomplete propodial was first identified as a 1.2 m femur [251] but turned out to be a 0.99 m humerus later [252]. McHenry [35] proposed 11∼12 m body length for this individual. However, if the propodial is indeed a humerus, its restored length is actually shorter than that of *Pliosaurus funkei*. The cervical and dorsal vertebrae, which might be lost in the last century [253], also indicate a similar size with the *Pliosaurus* model [251].

Fragmented fossils suggest that 9∼11 m pliosaurs were common in late Jurassic oceans of Europe. DORCM G. 123, an almost complete hindlimb, measures about 2 m in length and is comparative to the hindlimb of CAMSM J. 35990 [254]. Philips [255] listed some large anterior cervicals and referred them to *Pliosaurus macromerus* ([255]: p. 354, d, e, f; note that a, b, c have been provisionally recalassified to *P. brachydeirus* by Tarlo [110]). These three cervicals are by average 8% larger than corresponding vertebrae of the *Pliosaurus* model, suggesting a 10.5 m individual. The posterior cervical figured by Philips ([255]: Fig. 149) is comparative in length with the largest cervical of CAMSM J. 35990, thus its owner might be 9.8∼10.3 m in life. Sauvage [256] reported a complete pliosaur mandible that slight exceeds 2 m in length, which may come from an individual similar to or slightly smaller than the *Pliosaurus* model. Some large pliosaur materials discovered in the 18th and early 19th centuries were confused with the fossils of sauropods or other animals. For example, a posterior cervical (85 mm in length), which is slightly larger than corresponding vertebrae in the *Pliosaurus* model, was once misidentified as a sauropod and named as "*Cetiosaurus rigauxi*" [257]. Later Sauvage reclassified it to *Pliosaurus* [258]. Some French pliosaur materials bore the name "*Tapinosaurus*" in early literature [259, 260], and they were referred to *Pliosaurus* in a recent study [198]. Most of these large individuals were within the range of 9∼11 m ([259]: Plate 9, Fig. 2-3, Fig. 11).

Large pliosaurs also inhabited in the Jurassic oceans of South America. As stated in the preliminaries, body size of "the monster of Aramberri" was exaggerated. Its vertebral dimensions indicate that it was similar in size to the *Pliosaurus* model. Another pliosaurid from Caja formation, UANL-FCT-R7, comprises four and a half posterior cervicals, and their average length is approximately 90 mm [261]. Their maximum height and width are 145 mm and 140 mm respectively, indicating that they are suprisingly thin for thalassophonean cervicals (widths are typically twice the lengths of cervicals in late Jurassic pliosaurs [101]). To my knowledge, the only other example of such kind is the last two cervicals of the

holotype of *Brachauchenius lucasi* USNM 4989 [35]. In addition, the high positions of rib facets on the centra, together with the contact between centra and coracoid, make the "cervical" identification questionable ([261]: Fig. 9). If some of the four vertebrae are actually pectorals, then this individual might not be significantly larger than the *Pliosaurus* model due to the 91 mm pectoral in CAMSM J. 35990 [110]. Two large Tithonian pliosaurs (MOZ 6144P and MOZ 6141P) from Neuquén Basin, Argentina were briefly mentioned and classified to *Liopleurodon* sp. in a 1999 thesis [262]. MOZ 6144P had a 2.1 m skull, with a 4.6 m complex of cervical and partial dorsal series. The incomplete mandible of MOZ 6141P was 1.7 m along the ramus. Unfortunately, these two fossils were broken and lost before being studied (Zulma Gasparini, pers. comm, 2021). A precise estimation of body size is not applicable since the measuring criteria are unknown and no photos were provided in the original paper, but they were also likely to fall in the range of 9∼11 m.

There exist fossils indicating that some Kimmeridgian pliosaurs from Europe might far exceed the *Pliosaurus* model. OUMNH PAL-J.010454, a famous mandible that was classified to *Stretosaurus*, *Liopleurodon* and *Pliosaurus* before, was restored as 2875 mm in length [110]. Length of the imperfect mandible before restoration was 7 feet (about 2134 mm), as briefly mentioned by Prestwich [263]. There exists a breakage behind the dentary on each ramus of the mandible, and length of mandible anterior to breakage matches the value provided by Prestwich. Tarlo [110] argued that "...the posterior part of the left ramus has come to light... the total length would have been more than 3000 mm". There are indeed two associated lower jaw fragments from a single individual (OUMNH PAL-J.050376 and OUMNH PAL-J.050377) discovered in the same pit with OUMNH PAL-J.010454 and they match in size [264]. It is not certain which specimen Tarlo [110] referred to, but if it was OUMNH PAL-J.050376, total length of the mandible should be around 2.6 m (Shinya Noguchi, pers. comm, 2023). This suggests an individual which was 11.8 m, >20 t in size based on the *Pliosaurus* model. Prestwich [263] mentioned another large pliosaurid skull in Dorset Museum measuring 7.5 feet (about 2286 mm) long. This fossil, however, can no longer be traced (Shinya Noguchi, pers. comm, 2023). OUMNH PAL-J.010454 is not the only example indicating that Jurassic pliosaurs might reach or exceed 20 t. Martill et al [223] described four large posterior cervicals (ABGCH 1980.191.1038∼1041) from Abingdon, Britain. Comparison with the *Pliosaurus* model suggests this individual was 10.7∼11.8 m in body length. Another individual from Ely (YOYRM: 2006.19), described in the same paper, was 11.7∼13 m if the same method is applied. An isolated dorsal rib from France, housed in Museum of Le Havre, is 122 cm in chord length [198], suggesting a similar body size to the three individuals mentioned above.

7.2 A brief summary of plesiosaur body size evolution

A comprehensive analysis of plesiosaur body size evolution trends through deep time is beyond the scope of this study. Here I just present a brief description of body size evolution of different clades. Body sizes of all species other than the 22 models were estimated using Trunk-Volume or Dorsal Vertebrae-Volume regressions unless otherwise specified.

7.2.1 Rhomaleosauridae

In the early stage of their evolution, some rhomaleosaurids, represented by *Macroplata tenuiceps* (4.6 m, 0.92 t [195]) and *Atychodracon megacephalus* (5 m, 1 t [67]), were larger

than other Hettangian plesiosaurs. Smaller species like *Lindwurmia thiuda* (190 kg [265]) and *Avalonnectes arturi* (170 kg [22]) were also present. Sinemurian rhomaleosaurids like *Thaumatodracon wiedenrothi* [194] and *Archaeonectrus rostratus* [79] were generally smaller than their largest Hettangian relatives. The largest genus, *Rhomaleosaurus*, appeared in Toarcian [76]. Both *R. cramptoni* and *R. thorntoni* were around 6.8 m and weighed over 3 t [87]. There also exist fragmented materials suggesting that some rhomaleosaurids might reach 8 m [266]. After the faunal turnover between the early and middle Jurassic, the diversity and number of rhomaleosaurids droped drastically [267]. Only two valid rhomaleosaurid species are currently known from middle Jurassic: *Maresaurus coccai* [268] and *Borealonectes russelli* [148]. Despite their decline in number, some middle Jurassic rhomaleosaurids still retained large size. Assuming a same body proportion with *Rhomaleosaurus*, *M. coccai* and "*Trematospondylus macrocephalus*" might reach similar sizes with *R. cramptoni* and *R. thorntoni* ([268]: Fig. 1; [269]). *B. russelli*, on the other hand, was much smaller with an estimated body length of 3 m [148]. The youngest rhomaleosaurid fossils discovered so far are from Oxford Clay Formation, Callovian [270]. Their fossils, although fragmented, suggest large body size.

7.2.2 Pliosauridae

Early pliosaurids were small-headed and long-necked plesiosaurs. *Thalassiodracon hawkinsi*, an 1.5∼2 m long Hettangian species, was one of the smallest plesiosaurs [33]. Most pliosaurids from early Jurassic did not exceed 1 t in body mass, exemplified by *Attenborosaurus conybeari* (800 kg [50]), *Hauffiosaurus zanoni* (350 kg [271]) and *H. tomistomimus* (920 kg [53]). *H. longirostris* (2.9 t), on the other hand, was larger than the other two congeneric species [272, 22]. Shortly after the early-middle Jurassic transition, relatively large pliosaurids (possibly thalassophoneans) appeared in Bajocian oceans [273, 274, 247], probably to fill the apex predator niche left by rhomaleosaurids and *Temnodontosaurus* [267]. These macrophagous pliosaurids coexisted with relic rhomaleosaurids, which were similar to them in body size, till the extinction of Rhomaleosauridae in the end of middle Jurassic, but they probably employed different feeding strategies [275, 276, 138, 247]

It was in the Callovian that gigantic thalassophoneans (e.g., the Stewartby pliosaur, NHMUK PV R8322 [88]) first appeared. Body size diversity of pliosaurids also reached a peak in this period. Smaller species like *Liopleurodon ferox* (largest individual NHMUK PV R3536 around 8 m, 7.8 t [277]) and *Peloneustes philarchus* (holotype NHMUK PV R3318 about 650 kg [43]) were also present. The 9∼10 m range was frequently reached by late Jurassic pliosaurids (e.g., *Megalneusaurus rex* from Oxfordian [251, 134]; *Pliosaurus kevani* from Kimmeridgian [193]; *P. funkei* and *P. rossicus* from Tithonian [187, 278]). As discussed in the last section, some Jurassic pliosaurs might reach or exceed 20 t in life, accompanied by relatively small species like *P. brachyspondylus* (1.65 t [248]).

It has been revealed that the Jurassic-Cretaceous transition severely affected the evolution of Pliosauridae, and only one lineage, Brachaucheninae, crossed the boundary [20]. Little is known about pliosaurids from the beginning of Cretaceous due to poor fossil sampling. So far only two modest-sized brachauchenine species from Hauterivian have been erected: *Makhaira rossica* (1.05 t [279]) and *Luskhan itilensis* (2.87 t [216, 75]). Recent studies have revealed the abundant pliosaurid fossil records in the Southern hemisphere, especially South America [280, 74, 246] and Australia [35, 281, 282]. South American pliosaurids from Paja

Formation were diverse in both size and morphology: from short-snouted *Acostasaurus pavachoquensis* (4 m [283]), to piscivorous *Stenorhynchosaurus munozi* (8.65 m, 8.5 t [207]), to giant *Monquirasaurus boyacensis* (14 t [98, 74]) and *Sachicasaurus vitae* (17 t [39]). Opinions on the taxonomic status of a bunch of pliosaurids from Toolebuc Formation or Doncaster Formation, previously referred to *Kronosaurus* or *Eiectus*, haven't reached consensus (Espen Knutsen, pers. comm, 2022; Leslie Noè, pers. comm, 2022; and see [282] for a review of this issue). Despite the conflicting taxonomy, these brachauchenines were undoubtfully among the largest Cretaceous pliosaurs [35], with a maximum 15.5 t body mass.

Pliosaurid fossils from Cenomanian are rare, most of which were referred to the "waste-bascket" genus *Polyptychodon* [284]. The classification of *Polyptychodon* was generally based on tooth morphologies and its research history is chaotic [214]. As argued by McHenry [35], estimating body size from plesiosaur teeth is difficult and the results may be unreliable since tooth size varies across species and their positions in the jaws. However, a large tooth with 95 mm crown height (CAMSM B 75754) implies that giant pliosaurs existed in this period [284]. Some vertebrae described by Owen ([285]: p. 22-23) and a giant isolated cervical from Russia [286] also suggest that large pliosaurs around 10 m were present in Cenomanian oceans. They probably went to extinction together with the last ichthyosaurs [286]. Generally there is a consensus that pliosaurids went to extinction in middle Turonian [287]. Although some younger teeth were classified to *Polyptychodon* [284], the posibility that some "*Polyptychodon*" materials are actually polycotylids can not be ruled out [288]. Turonian pliosaurs were relatively modest in size. The holotype of *Brachauchenius lucasi* (USNM 4989) from Western Interior was 5.35 m, 2.2 t with SKL around 1 m [35, 289]. But some other materials referred to this genus indicate larger size. Both MNA V9433 from the Western Interior [290] (often referred to *B.* cf. *lucasi*; e.g., [23]) and an individual from Morocco [291] have cranial materials suggesting 1.5 m skull size, similar to the holotype of *Megacephalosaurus eulerti*. The paratype of *M. eulerti*, USNM 50136, contains partail skull elements from a larger individual, of which the DCL might be around 1.75 m in life [292]. It is the largest Turonian pliosaur discovered so far. Using the body proportion of coeval *B. lucasi*, USNM 50136 was around 9 m and 9.2 t. Therefore, some Turonian pliosaurids were still large in absolute size, although they were dwarfed by some early relatives like *Sachicasaurus vitae* [39].

7.2.3 Microcleididae and basal Plesiosauroidea

Basal pleiosauroids were present in the beginning of Jurassic, represented by *Eoplesiosaurus antiquior*, a 377 kg and long-necked species [22]. Small body size was retained in *Plesiosaurus dolichodeirus* from Sinemurian. NHMUK PV R1313 was around 3.5 m and 300 kg [293], and a humerus referred to *P.* cf. *dolichodeirus* by Dames indicates similar or slightly lagrer body size ([119]: p.8-10). *Westphaliasaurus simonsensii* (holotype about 4.5 m, 670 kg [294]) and *Eretmosaurus rugosus* (neotype NHMUK PV OR 14435 about 460 kg [79, 22]) were relatively larger. Most known microcleidids were from Toarcian, represented by *Microcleidus* spp. and *Seeleyosaurus guilelmiimperatoris* [22]. *S. guilelmiimperatoris*, *M. brachypterygius*, *M. melusinae* and *M. tournemirensis* were small species, not exceeding 350 kg in body mass [183]. The type species *M. homalospondylus* was much larger, with a maximum body length around 5 m [79]. In general, these basal plesiosauroids and microcleidids from early Jurassic presented a low size disparity pattern, as discovred by Benson et al [22].

7.2.4 Cryptoclididae

Cryptoclidids occurred in Bajocian, shortly after the early-middle Jurassic transition [267]. The earliest known cryptoclidid material is a propodial (MNHNL BM782), which is smaller than those of *Muraenosaurus* and *Cryptoclidus* ([267]: Fig. 10). Regressions based on propodial lengths or chords suggest that it was from a 350∼630 kg individual.

Abundant cryptoclidids occurred in Callovian, reaching high disparity in both morphology and body size [38]. From small *Tricleidus seeleyi* (266 kg) and *Muraenosaurus beloclis* (adult about 2.5 m in length), to medium-sized *Cryptoclidus eurymerus* (neotype NHMUK PV R2860 about 3.7 m and 440 kg; there exist materials 20% to 30% larger, which indicate >900 kg body mass [41]), to large *Muraenosaurus leedsi* (largest individual NHMUK PV R2425 up to 1.47 t [41]).

The flourish of this clade continued into late Jurassic. Two valid cryptoclidid species, *Pantosaurus striatus* and *Tatenectes laramiensis*, are known from Sundance Formation of Oxfordian [295, 296, 297]. *P. striatus* was a medium-sized species, with adult mass around 730 kg [81]. *T. laramiensis* was much smaller, with adult body mass just about 372 kg ([102]: Fig. 8). Some cryptoclidids travelled through the Carribean Seaway and reached South America during this period (e.g., *Muraenosaurus* sp. that weighed 985 kg [298]). Cryptoclidid fossils from Kimmeridgian Clay Formation are rather fragmented and incomplete, hiding the disparity of this clade [196]. The holotype of *Kimmerosaurus langhami* contains only a skull and several cervicals [38], thus it is difficult to estimate its size. *Colymbosaurus* was very large comparing with cryptoclidids from Oxford Clay Formation. For example, the syntypes of *C. megadeirus* (CAMSM J.29596etc) had a 1.7 m trunk indicative of 1.76 t body mass [196], and its body length was estimated as 5 m by Brown [38]. NHMUK PV OR 31787, the holotype of "*C. trochanterius*", might be 6.6 m in body length [38]. Thus the largest *Colymbosaurus* from Kimmeridgian Clay Formation might reach 4 t in mass. *"Plesiosaurus" manselii* (NHMUK PV OR 40106), estimated by Brown [38] to be 6.16 m in length, was within the size range of *C. megadeirus*.

Many cryptoclidid materials have been discovered in Slottsmøya Member of the Agardhfjellet Formation. As argued by Roberts et al [150], Cryptoclididae can be divided into Colymbosaurinae and an unamed subclade. The later contains some Tithonian species from Agardhfjellet Formation that possessed elongated necks. For example, *Spitrasaurus wensaasi* has 60 cervicals [299], which is within the range of elasmosaurids [48, 300]. The holotype of *S. wensaasi* was around 720 kg, and *S. larseni* was 4% larger. Osteological features indicative of immaturity explain the reason for their modest sizes. The cervical series of *Djupedalia engeri* is incomplete, but its estimated cervical count is 54 [301]. The holotype was also a juvenile at the time of death, weighing about 500 kg. The holotype of *Ophthalmothule cryostea* is an adult and possesses 50 cervicals [150]. However, vertebral dimensions suggest that it was just slightly larger than *Spitrasaurus* spp. at 790 kg. Colymbosaurines were also discovered from this formation, represented by *Colymbosaurus svalbardensis*. All individuals referred to this species were within the range of 1.3∼1.6 t [302, 105]. Besides the Agardhfjellet Formation, colymbosaurines are best known from Volgian Russia, with a high size disparity [303].

Morphologies of late Jurassic cryptoclidids indicate a preference for deepwater environments (e.g., *O. cryostea* [150]). This is consistant with the rise of global sea level during

that period [304]. The sea level changed rapidly and drastically during the earliest Cretaceous [305], which might lead to the decline of Cryptoclididae [306]. *Abyssosaurus nataliae*, a long-necked species from Hauterivian with adaptations for deep-diving [307, 135], was around 6.7 m, similar to the largest *C. megadeirus*. However, it was much thinner, weighing only 1.42 t. The youngest occurance of cryptoclidids was *Opallionectes andamookaensis* from Aptian of Australia, and the holotype was a 5 m juvenile [308]. In general, it appears that relatively large cryptoclidids with body mass over a t already occurred in middle Jurassic, and such a mass range evolved repeatedly in different species from late Jurassic and early Cretaceous.

7.2.5 Elasmosauridae

This clade is known for extremely long necks (over 70 cervicals in some taxa [171, 55]). Gutarra et al [4] proved that large body sizes can compensate for extra drag caused by long necks. Indeed, elasmosaurids were larger than other groups of long-necked plesiosaurs, possibly able to reach 13 m in length (see below). But girdle dimensions suggest that they were very slim animals. For example, width of coracoid at hinder angle of glenoid in *Elasmosaurus platyurus* is less than that of a 4.3 m *Peloneustes philarchus* [34, 111]. No elasmosaurid examined in this study exceeded 10 t, thus they are dwarfed by the largest pliosaurs (>20 t). Welles [36, 34, 214] offered body length estimates for many elasmosaurids, but most of them contained no intervertebral cartilages. Therefore, his results should be used with caution.

There were only a few valid elasmosaurid species from the early Cretaceous, and their fragmented fossils often preclude body size estimation. *Jucha squalea*, a Hauterivian species with 1.65 t body mass, was modest in size for elasmosaurids [309]. *Callawayasaurus colombiensis* from Paja Formation was around 8.2 m, 2.46 t [214]. *Wapuskanectes betsynichollsae* from Clearwater Formation was the largest early Cretaceous elasmosaurid examined in this study [52]. Coracoid width suggests it was 3.18 t in body mass. Kear [147] argued that Australian elasmosaurids require a broad revision on both taxonomy and phylogeny, and many materials are undiagnostic to date [282]. Some extremely small juvenile elasmosaurids (body length <2 m) are known from early Cretaceous of Australia [310], while larger individuals around 6∼7 m have also been discovered [308]. The holotype of *Eromangasaurus australis*, QM F11050, was probably bitten and killed by a large pliosaur [311]. It is difficult to estimate its body size due to its incompleteness. Generally speaking, most elasmosaurids from early Cretaceous were modest in size, and they coexisted with similar-sized relic cryptoclidids like *Opallionectes andamookaensis* [310].

Large elasmosaurids occurred in the earliest late Cretaceous. *Thalassomedon haningtoni* from Cenomian weighed over 7 t thanks to its large trunk [36]. *Libonectes morgani* from Cenomian-Turonian was much smaller (holotype around 8.3 m using the ratio of referred individual SMNK-PAL 3978, which was 7.2 m in length [312, 313]). Many elasmosaurid species have been discovered from Campanian of the Western Interior Sea in North America. These elasmosaurids are characterized by their elongated necks, and were once thought by previous researchers to form a monophyletic clade, Elasmosaurinae (= "Styxosaurinae") [212, 149]. However, it has been suggested that some characters supporting this clade might be homoplastic [309]. Both *Albertonectes fernandezi* and *Elasmosaurus platyurus* possessed over 70 cervicals [46, 55] and were large in size (*A. fernandezi* about 12.1 m, 4.46 t; *E. platyurus* about 11.4 m, 4.43 t). One major taxon from the Western Interior

Sea is *Styxosaurus*. *Styxosaurus* sp. SDSM 451 was selected as a basic model (Table 2). Vertebral dimensions suggest that *S. snowi* KUVP 1301, *S. browni* AMNH 5835 and *"Hydralmosaurus serpentinus"* AMNH 1495 were all within the range of 3.5∼4.5 t. *Styxosaurus rezaci* from Cenomanian was previously referred to *Thalassomedon haningtoni*, and they were similar in body proportions [314]. Using the model of *T. haningtoni*, the body mass of *S. rezaci* was around 9 t [315]. It is the largest non-aristonectine elasmosaur to my knowledge. Fragmented materials from other large elasmosaurids have also been discovered from Niobrara Chalk. KUVP 1302 and KUVP 1312 (which was overestimated as >18 m by Williston [316]) were both around 6 t in life [34]. Welles [214] argued that "*Plesiosawrus helmersenii*" from Senonian is the largest elasmosaur, but vertebral sizes indicate a 6∼7 t mass [317], which is exceeded by *T. haningtoni*. Using the ratio of *Styxosaurus* SDSM 451, "*P. helmersenii*" might reach or exceed 13 m in length. Elasmosaurids also existed in North America during Maastrichtian, exemplified by *Hydrotherosaurus alexandrae* (8.8 m, 2.3 t [36]) and *Nakonanectes bradti* (5.1∼5.6 m, 1.6 t [318]).

Studies in the past decade have revealed the diversity and broad distribution of Weddellonectia, the major elasmosaur clade during Maastrichtian [212, 107]. Species of this clade have been discovered in North America (e.g., 2.8∼4.6 t *Morenosaurus stocki* [36]), Asia (2.2 t *Futabasaurus suzukii* [106]), New Zealand (>8 m *Tuarangisaurus keyesi* [108, 319]), South America (3.8∼4.2 m *Kawanectes lafquenianum* [66]) and Antarctica (6.2 m, 1.25 t *Vegasaurus molyi* [300]).

Besides these modest-sized species, a derived subclade of Weddellonectia, Aristonectinae, is characterized for shortening of the neck [212, 184, 127]. The body size estimation of *Aristonectes* metrits a review. Most of our knowledge on postcranial elements of this genus comes from *A. quiriquinensis*, of which the fossils are sufficient for constructing a mixed model (Fig. 1A). It should be noted that attribution of this species to *Aristonectes* has been revealed to be questionable, and more complete materials are needed to clarify its relationship with the type species [320]. Otero et al [109] proposed a vertebral formula which contains 40∼42 cervicals and 20 dorsals without mentioning sacrals or pectorals. They estimated the body length of the holotype at 9 m. Otero et al [127] later suggested 43 cervicals, 3 pectorals, 23 or 24 dorsals, 2 or 3 sacrals and 35 caudals for this species. They also calculated the forelimb as 3 m and trunk as 4 m, which were adopted in some recent studies (e.g., [4]). However, it can be noticed that the body proportions summarized from their calculation don't match the silhouette reconstruction ([127]: Fig. 10). O'Gorman et al [149] adopted the vertebral formula proposed by Otero et al [127], and re-estimated the body length of holotype at 10.232 m. They also reported a larger individual MLP 89-III-3-1, which is referable to *Aristonectes* sp., and estimated a body mass over 10 t using the *Cryptoclidus* model constructed by Henderson [215]. Trunk lengths of both individuals were estimated as being much shorter than 4 m by them. A model for *Aristonectes* was created under the criteria proposed in this paper and was based on *A. quiriquinensis* (Table 2; see supplementary materials for detailed process). Here I also confirm that no elasmosaur had the potential to possess a 4 m trunk among all the fossils reviewed in this study. The body mass of MLP 89-III-3-1 is reduced to 9.2 t due to the thinner rib cage comparing with *Cryptoclidus*, but it remains the largest elasmosaurid known to date, followed by *Styxosaurus rezaci* USNM 50132. The holotype of *Aristonectes parvidens*, MLP 40-XI-14-6 [184], was estimated here at 8.5 m by comparing its cervical dimensions with *A. quiriquinensis* holotype.

Besides giant *A. quiriquinensis*, a small taxon, *Morturneria seymourensis*, was also discovered from the López de Bertodano Formation. SKL of the holotype was estimated at only three fourths of that in adult *A. quiriquinensis* [321]. Although the holotype of *M. seymourensis* is osteologically immature, another older specimen helps confirm the small size of this species [322]. *Kaiwhekea katiki* is known from an articulated specimen discovered in New Zealand [323]. Attempt to construct a model for this taxon is hampered by the missing or poorly preserved girdle elements. Its trunk length indicates a 2.5 t body mass.

7.2.6 Polycotylidae

The phylogeny and taxonomy of Polycotylidae has been revised very recently by Clark et al [176], and I follow their taxonomic system despite the unstable topologies inside this clade discovered in previous studies [324, 213, 325, 326]. The earliest polycotylids are known from Aptian of Australia [327]. Other materials from early Cretaceous include *Edgarosaurus muddi* from North America (estimated at 3.2∼3.7 m by Drunkenmiller [222]), the "Richmond pliosaur" from Australia and some indeterminate fossils [310, 328]. The key turning point of polycotylid evolution was the Cenomian-Turonian transition, which marked the extinction of some basal lineages (e.g., Occultonectia [326], contra [213]) and the rise of polycotylines. The body size disparity within Polycotylidae was also very high during this period, caused by the existence of species from different lineages which varied greatly in body mass: from the 400 kg *Scalamagnus tropicensis* [329], to 730 kg *Palmula quadratus* and 865 kg *Eopolycotylus rankini* [324], to large *Trinacromerum bentonianum* which weighed over 1.5 t [70]. Although polycotylids were traditionally considered as representatives of "pliosauromorph", some species during this period possessed relatively long necks, exemplified by the 1.58 t *Thililua longicollis* from Morocco [330]. It has been revealed that long necks evolved in polycotylids for several times [213], and this body plan existed till end of Cretaceous (e.g., *Serpentisuchops pfisterae* [331]). A long neck was also present in *Polycotylus latipinnis* which was 4.7 m, 1.15 t [218]. The most derived and recently named subclade of Polycotylinae, Dolichorhynchia [176], contains some relatively short necked species like *Dolichorhynchops* spp., which were 400∼500 kg in body mass [78, 197, 332]. *Unktaheela specta* was tinier, possessing the smallest skull among all adult polycotylids [176]. On the other hand, large dolichorhynchians like *Martinectes bonneri* (4.5 m, 1.45 t) were also present in late Cretaceous [333, 190]. Fossil records imply that polycotylids declined significantly before the end of Maastrichtian, and the reason remains unclear in the current stage [213].

7.2.7 Leptocleididae and freshwater plesiosaurs from China

In addition to their flourish in marine environments, multiple plesiosaur lineages entered freshwater or marginal habitats and radiated there [201]. One clade of iconical freshwater plesiosaurs, Leptocleididae, is characterized for their relatively short necks and small body sizes [334]. This family was once regarded as a subclade of Pliosauroidea, but has been revealed as a lineage of Xenopsaria in recent phylogenies [20, 213]. The type genus, *Leptocleidus*, was estimated to be 2.5∼3 m in body length in previous studies [61, 335]. *L. clemai*, with 400∼440 kg mass, was the largest species of this genus, followed by 277 kg *L. superstes*. The smallest *L. capensis* was only around 200 kg. There exist some fossil materials referable to *Leptocleidus* but undiagnostic at species level, and they all indicate

small body sizes [201]. Besides freshwater species, leptocleidids are also known from marine environments. *Umoonasaurus demoscyllus* was a small marine species (about 2.5 m) which inhabited in a seasonally near-freezing region [336]. Another marine species, *Nichollssaura borealis*, is known from a 2.6 m articulated skeleton discovered from Clearwater Formation [337].

Fossils of other plesiosaur clades have also been found in freshwater or marginal environments (e.g., [82, 104]). A review of these materials have been carried out by Bunker et al [201]. Therefore, I don't re-examine all these fossils but focus on body sizes of freshwater plesiosaurs from China. Many of them were described using chinese in the last century and have never been included in phylogenies, thus a broad revision is desirable but beyond the scope of this study. The phylogenetic affinity of *Bishanopliosaurus youngi* is unclear since the holotype is an osteologically immature individual which shows both rhomaleosaurid and pliosaurid features [338]. Dong [339] offered a 4 m length estimate, and vertebral dimensions indicate a 600 kg body mass. Another species, *B. zigongensis*, is known from the type specimen which contains 20 articulated dorsals, 2 sacrals and incomplete pelvic girdles and limbs [340]. The articulated dorsal series measures 770 mm, which is slightly over one third of the trunk length in *Rhomaleosaurus thorntoni* [67]. All species of *Sinopliosaurus* were established on very fragmented materials, making their validity suspicious [341, 342]. Buffetaut et al [343] reviewed these materials and argued that the type species *S. weiyuanensis* is a *nomen dubium* and *S. fusuiensis* is actually a spinosaurid. Another species, *S. sheziensis*, was established on extremely fragmented materials including teeth, incomplete ribs and sacral vertebrae [344], which might be undiagnostic as well. In general, the validity of *Sinopliosaurus* remains doubtful, and it is difficult to carry out body size estimation due to the poor preservation of fossils. But all current materials indicate small body sizes. An incomplete mandible is preserved in the holotype of *Yuzhoupliosaurus chengjiangensis*, which represents the only plesiosaur cranial material discovered in China so far. Zhang [345] reconstructed the complete length of mandible at 540 mm and estimated total body length at 4 m. Dimensons of its dorsal centra suggest a 663 kg body mass. Freshwater plesiosaur fossils were also discovered from Xinhe Formation and Xintiangou Formation of China, most of which are undiagnostic teeth or vertebrae [346, 347].

7.3 Enlightment for future studies

This study is the first attemp to develop a uniform set of body reconstruction criteria for the whole Plesiosauria with quantitative restoration of cross-sectional profiles. Zhao [234] argued that careful reconstructions of body cross-sections are required in body mass estimations since simply assuming elliptical or superelliptical approximations may incorporate errors. Although the criteria proposed in this study are restricted to plesiosaurs, similar methods can be developed for precise body reconstruction of other extinct vertebrates including dinosaurs and other marine reptiles.

Body mass and surface area of an animal are linked to many of its biological properties. There is a growing trend in the past decade to use fluid dynamic methods like Computational Fluid Dynamics (CFD) or experiments to study the hydrodynamic performances of plesiosaurs (e.g., [73, 161, 4]). Results of these studies would be affected by body shapes, thus rigorous reconstructions would help clarify many physiological features of

plesiosaurs (e.g., optimal swimming speed) and lead to a better understanding of variation in locomotory strategies applied by different clades.

This study also offers several scaling equations for quick body mass estimation, which allows predicting body size from very fragmented fossils. Mass is a better proxy for body size than length since plesiosaurs display diverse body proportions. After quick obtainment of mass information, these results can be imported to subsequent morphometric studies to control for allometry, which is necessary because body masses of plesiosaurs range from several hundred kilograms to over 20 tonnes. These tools also enable the study of plesiosaur body size evolution through deep time and help illuminate the whole picture of their 135-million-year story.

8 Conclusions

Body mass estimations of plesiosaurs were scarce and were carried out under different criteria in previous studies. Some published results were just rough estimates based on models with questionable reliability. The burst of plesiosaur studies in the past two decades has offered sufficient information for the development of an uniform set of reconstruction protocols. During this process, some correlations between plesiosaur skeletal elements were revealed.

Twenty two models were created under this set of criteria. Linear regressions based on these models illuminate that there exist positive corrlations between plesiosaur skeletal elements and body volume. The scaling equations can thus been applied for quick body mass prediction using very fragmented materials.

The maximum body length of Plesiosauria was probably 13 m, which was reached by both elasmosaurids and pliosaurids juding from fragmented materials. The heaviest plesiosaurs examined in this study are some Jurassic pliosaurs with body masses over 20 t. On the other hand, the smallest adult plesiosaur weighed less than 200 kg, revealing the high body size disparity of this clade. This study is a staring point of a comprehensive research on plesiosaur body size evolution.

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